

AN ABSTRACT OF THE THESIS OF

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Long-term oceanographic and meteorological data were used to develop models that describe the observed variation in the recruitment of Pacific mackerel (*Scomber japonicus*) in the California Current region. The models that were found to best describe recruitment included both density-dependent factors and environmental factors. Models incorporating only density-dependent factors accounted for a maximum of 24 percent of the observed variation in recruitment. Multiple regressions models including both density-dependent and environmental-dependent factors were fitted to the data available for two time periods; 1931-1968 and 1946-1968. A model including three environmental factors and a density function was selected as the best fit to the longer period. In this model increased recruitment was associated with increased sea surface temperature, reduced sea level, and reduced atmospheric pressure during the spawning season. This model accounted for 59 percent

of the variation in recruitment from 1931-1968. The model fitted to the 1946-1968 period included a density function and two environmental factors, on which data was not available prior to 1946. Increased recruitment with this model was associated with increased coastal upwelling and decreased offshore convergence during the spawning season. This model accounted for 76 percent of the variation in recruitment from 1946-1968.

Yield per recruit simulations gave greatly different results than dynamic pool simulations. Maximum yield with a yield per recruit model occurs with an age at recruitment of 1 or less and instantaneous fishing mortalities (F) in excess of 1.0. Dynamic pool simulations that incorporate a Ricker spawner-recruit function predict that extinction of the stock will occur with the above fishing strategy. Dynamic pool simulations with both density-dependent and environmental-dependent recruitment functions were assessed to determine maximum yield with different ages at recruitment and different quota options.

An Assessment of Environmentally Related Variation in the
Recruitment of the California Current Stock of Pacific Mackerel
(Scomber japonicus) and its Implications for Management

by

Richard Henry Parrish

A THESIS

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Oregon State University

in partial fulfillment of
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degree of

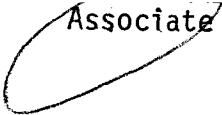
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AN ASSESSMENT OF ENVIRONMENTALLY RELATED VARIATION IN THE
RECRUITMENT OF THE CALIFORNIA CURRENT STOCK OF PACIFIC MACKEREL
(Scomber japonicus) AND ITS IMPLICATIONS FOR MANAGEMENT

INTRODUCTION

The objectives of this work are to assess the role of environmental variation in the decline of the California stock of Pacific mackerel (Scomber japonicus) and to evaluate the merits of using environmental data in management policies for this species. The study is principally focused upon two areas. The first is the development of density and environmental-dependent regression models that describe recruitment in the above stock. The second is the use of these regression models in dynamic pool computer simulations to describe the types of management policies that are likely to both decrease the possibility of another recruitment failure and maximize the long-term yield from the stock.

Over the last decade there has been increased attention focused on the stock and recruitment problem of commercially important fishes. If any consensus can be obtained from the large amount of published data available, it is that the major factor affecting recruitment is larval survival. The mechanisms controlling larval survival, of course, may vary from stock to stock. Some workers suggest that a critical stage occurs at the time of first feeding (Hjort 1926; Lasker 1965). Other workers feel that the critical period extends for up to 45 days (Jones and Hall 1973).

Most of the recent research into the recruitment problem has been divided into two phases: laboratory and field experiments on larval fish biology, and population dynamics models. The development of models has been dominated by conceptual work; a statistical approach to the problem has been limited by the lack of long-term data on both fish populations and environmental conditions. Long-term data is becoming available for statistical analyses and workers are beginning to develop multiple regression models utilizing environmental and density-dependent variables (Nelson et al. 1976, Lett et al. 1975). One of the best long-term data bases available for statistical analyses of the associations between recruitment of pelagic fishes and environmental conditions is that of the California Current region. This extensive data base is largely the result of the multidisciplinary approach of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

I have used the CalCOFI data base to determine associations between the recruitment of Pacific mackerel and environmental variables. Recruitment models including density parameters and both density and environmental parameters were then developed with regression procedures. These recruitment models were incorporated in computer simulation models to assess the differences in their predicted yields. The results of the simulations were then analyzed to examine the relative merits of managing the fishery on two different policies; that is, policies based on a yield per recruit model and policies based on dynamic pool simulations incorporating both density-dependent and environmental-dependent factors.

Previous work on recruitment in Pacific mackerel has been limited to density-dependent recruitment models. Ricker spawner-recruit models were described by Blunt and Parrish (1969) and Parrish (1974). The present work is the first to incorporate long-term environmental data in recruitment models of a California Current stock and to use observed environmental data to drive simulations using such models.

DATA SOURCES

HISTORY OF THE FISHERY

The development and subsequent decline of the Pacific mackerel fishery has been well documented in the literature. Croker (1933) discussed the early history of the fishery including fishing areas and the development of mackerel canning in California. Descriptions of the fishery during and after its peak include those by Croker (1938), Roedel (1952), Fitch (1952), and Roedel and Joseph (1954). The fishing gear used in the fishery was principally round-haul gear and scoop gear (Fry 1931; Croker 1933; and Scofield 1947, 1951). More recent reviews of the fishery include Blunt and Parrish (1969), Kramer (1969), and MacCall (1973). Status reports showing current condition of the stock were prepared by Frey and Knaggs (1973) and Knaggs (1974).

The commercial landing statistics of Pacific mackerel show a rapid increase during the early 1930's to a peak of over 146 million pounds in 1935. The landings then show a cyclic decline to near commercial extinction by the early 1970's when a moratorium halted the fishery (Figure 1). The sport landings of Pacific mackerel have always been of relatively minor importance in the total marine sport landings. Young (1969) ranked them as the eleventh most important species in the southern California partyboat fishery and the mean catch from 1947-1967 was 127,921 fish. Only trace amounts of Pacific mackerel occur in the northern California partyboat catch.

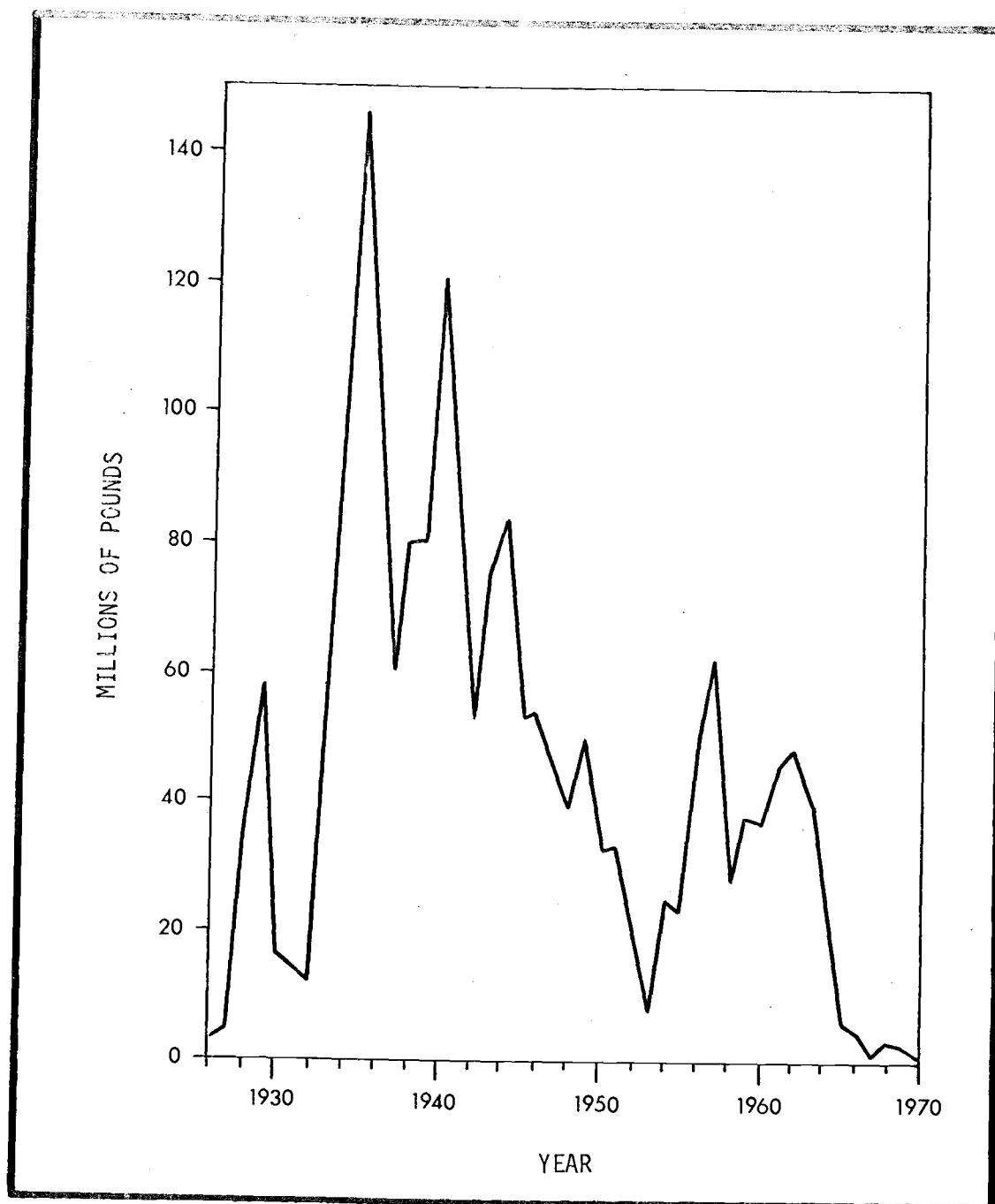


FIGURE 1 Pacific mackerel landings in California (1926-1970)

Pinkas et al. (1968), who ranked the most important sport caught fish for southern California marine waters from 1963-1966, found Pacific mackerel to be the eighth most important species in the total marine sport fish catch, where it comprised 3.2% of the fish caught.

MANAGEMENT OF THE FISHERY

Attempts to control or manage the Pacific mackerel fishery were unsuccessful until the stock had collapsed. A moratorium was then enacted by the California Legislature. During the period of 1936-1970 research personnel working on the stock, principally from the California Department of Fish and Game and later including the National Marine Fisheries Service and Scripps Institute of Oceanography, made several major attempts to control the fishery. Management proposals generally concerned both the Pacific mackerel and sardine. Blunt and Parrish (1969) have discussed the past management proposals for Pacific mackerel. An excellent review of the sardine-anchovy regulation controversy was given by Talbot (1973) and much of his account of the sardine is equally true for Pacific mackerel. Messersmith's (1969) treatment of the anchovy controversy provides considerable documentation of the problems of managing the pelagic fisheries of California.

The most recent attempt to regulate the Pacific mackerel fishery was associated with the anchovy-sardine controversy and began about 1967. At this time it became obvious that the spawning biomass of Pacific mackerel was declining rapidly due to a long series of years

with poor recruitment. Warnings of this decline (Parrish 1968; Blunt and Parrish 1969) and of the continuing critical situation with the sardine (Aasen 1967) accompanied the descriptions of underexploited species such as the anchovy (Messersmith et al. 1969; Ahlstrom et al. 1967), squid, (Longhurst 1969) and saury (Smith and Ahlstrom 1970). The scientific community was in the politically unenviable position of arguing for increased harvest of the anchovy at the same time it was recommending complete closure of the commercial fishery for sardine and Pacific mackerel.

In response to continuing requests to enact moratoriums on Pacific mackerel and to halt the bait fishery on sardine, the California Legislature requested the California Department of Fish and Game to arrange meetings with Mexican scientists to determine the exact status of the resource (MacCall 1973). In the fall of 1972 cooperative research was undertaken. However, the continued decline of Pacific mackerel off of California and the increasing fishing mortality, which had by then become very heavy even on age 0 Pacific mackerel, encouraged the California Legislature to enact a unilateral moratorium on the commercial fishery for Pacific mackerel. This moratorium allowed an 18% tolerance for Pacific mackerel in mixed loads.

In 1972 the California Legislature enacted a bill that imposed a quota based on the spawning biomass of the Pacific mackerel. The regulation maintains a moratorium until the spawning biomass exceeds 20 million pounds. If the spawning biomass exceeds 20 million

pounds (lower quota level) the annual quota consists of 20% of the excess over 20 million pounds. If the spawning biomass exceeds 40 million pounds (upper quota level) the quota consists of 20% of the amount between 20 million and 40 million pounds plus 30% of the excess over 40 million pounds.

Estimates of the 1974 spawning biomass of Pacific mackerel were given by Knaggs (1974). He reported that the estimate derived from tagging studies was 4.05 million pounds. His alternative estimates were derived from linear regressions of the partyboat catches in two areas and the spawning biomass estimates from the period of 1956-1966. These estimates were 9.35 and 16.76 million pounds.

ENVIRONMENTAL VARIABLES

The choice of environmental variables to include as potential variables in recruitment functions for Pacific mackerel was largely dependent upon available long-term data. Unfortunately such data were not available on plankton populations. Data sources were therefore limited to physical oceanographic and meteorological data.

Environmental data analyzed can be grouped into three general categories based on the period of coverage. Category one includes land-based meteorological, sea level and sea surface temperature data. The period covered by these data includes the entire period of the data base of the population estimates (1928-1968). Data analyzed included monthly mean atmospheric pressure at San Diego, mean sea level difference between San Francisco and Hilo, Hawaii

(Saur 1973), monthly mean sea surface temperature at Scripps Pier, and the monthly mean sea level at La Jolla. Sea level data were included as a potentially important variable because of the relationship between geostrophic flow and coastal sea levels. Reid and Mantyla (1976) have shown a close relationship between seasonal geostrophic flow and sea level elevations at La Jolla, California.

The second category included ship observation data. These data are available as monthly means by 5 degree blocks (i.e., Marsden Square quadrants). The data base starts in 1931. Data analyzed included wind speed, sea surface temperature, and cloud cover for Marsden Square quadrants 120 (2) and 84 (3) (Figure 2). All of the data for Marsden Squares and for sea level at La Jolla was provided by the Pacific Environmental Group of the National Marine Fisheries Service. Data on wind speed were included as it would be expected to be related to upwelling. Cloud cover could be important in that it might be used as an index of insolation and it could also be related to upwelling.

The third category is composed of data from a series of mass transport calculations. The data were provided by Bakun (pers. comm.) and his calculations were made with the calculation procedures described by Fofonoff (1960). Data analyzed included meridional total transport, meridional Ekman transport, divergence of Ekman transport (Bakun's (pers. comm.) offshore divergence indices), and Bakun's (1973) coastal upwelling indices (i.e., Ekman transport perpendicular to the coast). The transport calculations were based

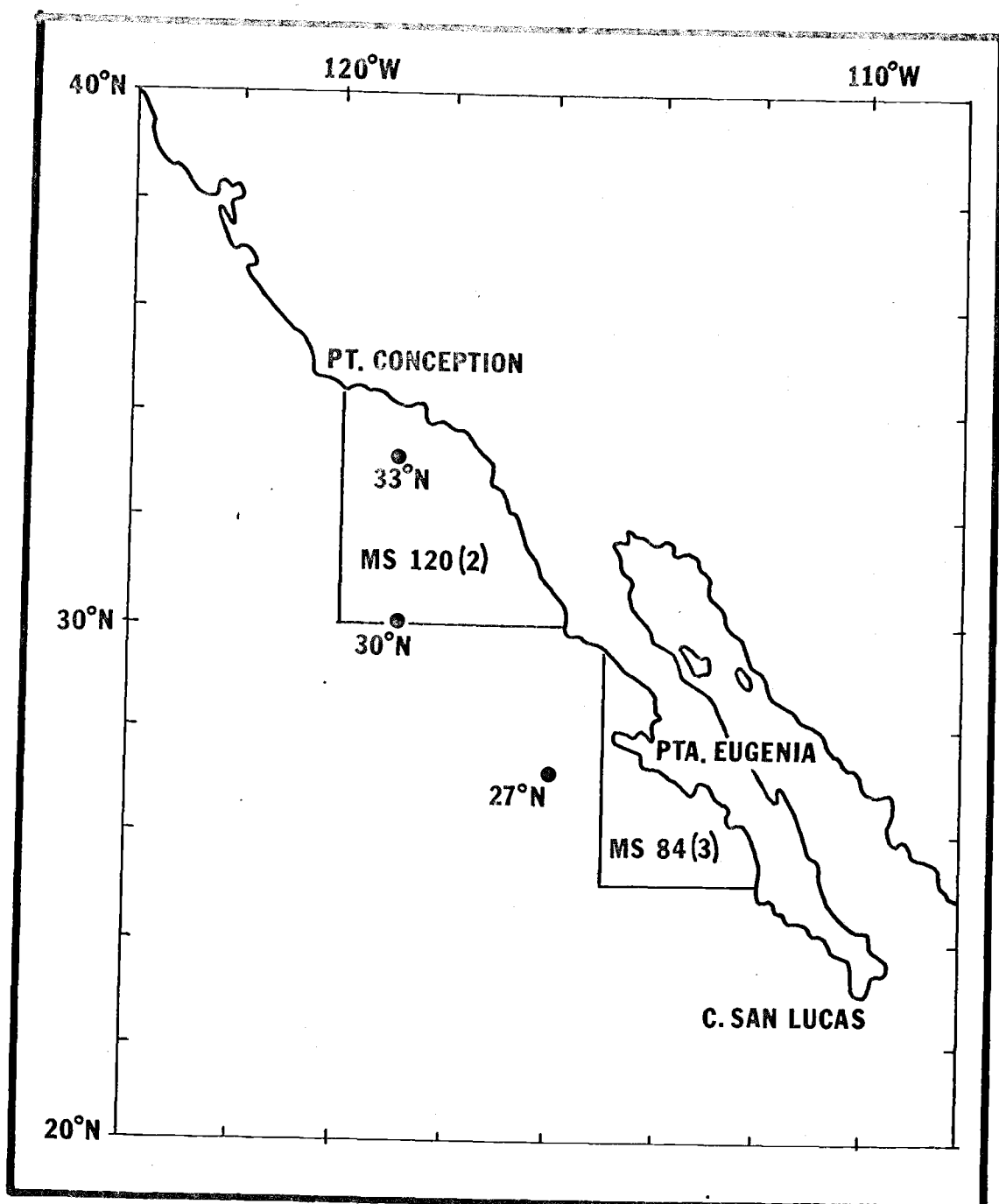


FIGURE 2 Marsden Square quadrants 120(2) and 84(3), and upwelling index locations

on a 3° grid of monthly mean atmospheric pressure that was interpolated from pressure fields prepared by Fleet Numerical Weather Central. The data base starts in 1946. Analysis of the transport data included the calculations at three locations; 27°N , 30°N and 33°N (Figure 2). Nelson et al. (1976) have shown that Ekman transport, calculated by Bakun's (1973) methods, accounts for 84 percent of the variation from a Ricker spawner-recruit curve in Atlantic menhaden.

The four sets of transport data are actually indices of two processes. Bakun's (1973) upwelling indices and meridional Ekman transport are different angular components of wind-driven transport. The units of measure in these components are metric tons per second per 100m width. The second mechanism is wind stress curl, which is a measure of the rate of change of wind driven transport with respect to space. Sverdrup (1947) has shown that meridional total transport is proportional to wind stress curl. The divergence of Ekman transport, which is proportional to total meridional transport minus meridional Ekman transport, is dominated by total transport and is therefore essentially the same as wind stress curl. Units of the two measures of wind stress curl are given in terms of vertical velocity (millimeters per day, positive upwards) through the bottom of the Ekman layer.

POPULATION BIOLOGY

Growth

A very large volume of data is published on the age composition of the southern California catch of Pacific mackerel and annual growth in length is well documented. However, documentation is lacking on the seasonality of growth and on growth in weight generally. Individual weights were not recorded for the market samples until the mid 1960's. In addition published age-composition data represent a composite of information for the entire season.

Bertalanffy growth equations and length-weight relationships were calculated by Knaggs and Parrish (1973) for data from the 1958-1959 to 1969-1970 seasons. They reported that there were no significant differences at the 99% level between their data and Fry's (1936b) data. They also reported little correlation between 29 years of estimates of recruit abundance and mean size at age 1 ($r = -0.208$). However, it should be noted that a good comparison (i.e., weight at a given age) is lacking. In this instance mean size at age 1 means the mean length of fish sampled during the season (i.e., May 1-April 30) and this mean age may vary from year to year due to availability or seasonal variations in fishing pressure.

The growth estimates used in the present paper are the Bertalanffy growth equation and the length-weight relationship given by Knaggs and Parrish (1973). Both annual growth and weight

at capture were used in simulation models. Weight at the beginning of the season (May) was used to calculate spawning biomass and annual growth. Weight at capture was used to calculate catch. Length at the first birthday, with the Bertalanffy equation as fitted by Knaggs and Parrish (1973), is calculated with $t = 0.5$ and the length of age 1 fish at capture is calculated with $t = 1.0$. This correction is necessary due to the fact that the Bertalanffy equation was calculated with the criteria for age 1 being all fish between the ages of 1 and 2. The Bertalanffy estimate with $t = 1.0$, therefore, is an estimate of length at an age of 1.5 years.

Reproduction

Age at maturity and percent spawning by age group were not well documented during the early fishery. According to Fry (1936b) "the yearling fish do not spawn whereas most of the two-year-olds do." Fitch (1951) stated that most mackerel do not spawn until their third or fourth year. For the period of 1958-1970 Knaggs and Parrish (1973) found that 22.5%, 65.7%, 75.1%, 84.7%, 84.2%, and 87.0% of age group 1 through 6+ sampled during the period of April-August were mature or maturing.

The above percentages represent minimum percentage maturity, as early spawners might have completed spawning when captured in August or late spawners might be immature when captured in May. Therefore, in the present work I have decided that it is most realistic to assume that 100% of the fish of age 4 or older are

mature. The percentages mature of ages 1, 2, and 3 were increased by the same proportion as ages 4+ (i.e., 0.17). This results in percentages of 26%, 77%, and 88% for ages 1, 2, and 3.

The major inconsistency between the data taken in the early fishery, when biomass levels were high, and the late fishery, when biomass levels were low, is the percentage of age 1 fish that spawn. The Fry (1936b) and Fitch (1951) data were taken when biomass was high. The percentages mature reported by Knaggs and Parrish (1973) are average values taken over the period 1958-1959 to 1969-1970, when biomass varied from moderately high to very low levels. In an attempt to determine if the percentage of age 1 fish spawning depends on density, the original market samples used by Knaggs and Parrish (1973) were analyzed to see if a pattern could be determined. Maturity stages were not recorded in market samples prior to 1958-1959, and in individual samples these data were sometimes missing for several years thereafter. When analyzed by individual year the numbers became so small that validity was questionable. However, during the period 1969-1971, when the spawning biomass was at extremely low levels and there were large numbers of age 1 fish sampled, 50% of the age group 1 fish were mature or maturing.

The available information suggests that there is an inversely density-dependent relationship between population size and the percentage of age 1 fish that spawn, although the exact form of this relationship is difficult to demonstrate. It appears that the percentage of age 1 spawners can be approximated at three general

biomass levels (Figure 3). An exponential curve fitted to these points gives the following relationship, which was used in the regressions to determine recruit-spawner functions and in all simulations.

$$PS = 0.540 e^{-0.00717 \text{ TPOP}}$$

where PS = proportion of age 1 fish spawning

TPOP = total population biomass in millions of pounds

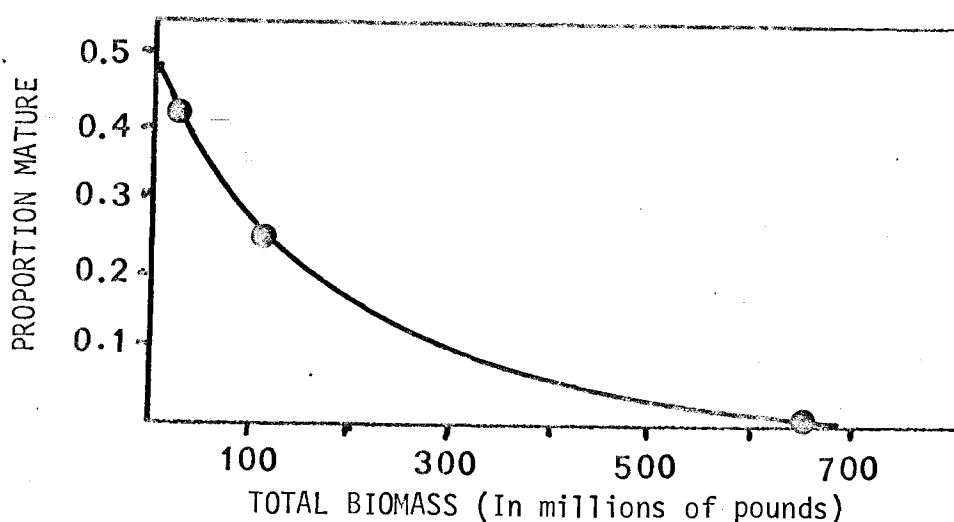


Figure 3 The relationship between total biomass and the proportion of AGE 1 spawners

There is an alternate hypothesis to explain the increasing percentage of age 1 fish that spawn at low biomass levels. Fry (1936b) stated that a small proportion of fish in the southern Baja stock spawned at age 1. It is possible that a small number of fish from the southern Baja California stock enter the California fishery. These fish could provide an increasing proportion of the mackerel available to the California fishery as the northern stock

declined to the very low levels of the late 1960's. Tagging studies neither confirm nor invalidate this alternate hypothesis, because fish south of Central Baja were not tagged during the major tagging work carried out by Fry and Roedel (1949) or in more recent work (Knaggs 1974).

The eggs and larvae of Pacific mackerel are pelagic. The eggs hatch approximately three days after fertilization, depending on temperature (Fry 1936a). Fry (1936b) found most of the eggs to be spawned in water less than 88 m deep and between 16.7° and 20.6°C (62° and 69°F). Ahlstrom (1959) suggests that spawning occurs closer to the shore and closer to the surface in Pacific mackerel than in the other major pelagic species in the California Current region. Kramer (1969) reported that the abundance of Pacific mackerel eggs fell off sharply below 23 m. Estimates of fecundity in Pacific mackerel are based on relatively few individuals. MacGregor (1966) reported that the Pacific mackerel produces 304 eggs per gram of fish (based on counts for six specimens). MacGregor (1975) reported that 18 Pacific mackerel averaged 259 eggs per gram. He suggested that a lower estimate of fecundity per body weight was associated with first-time spawners in a number of species but he did not report that this occurs in Pacific mackerel.

Fry (1936a) found that Pacific mackerel eggs varied in size during the spawning season; eggs were larger in April-May than in June-July. The data on age at maturity reported by Knaggs and Parrish (1973) showed that spawning of older mackerel peaks in

May while in age 2 it peaks in June and in age 1 it peaks in July. Bakun (1973) shows that peak upwelling in Central Baja occurs in May. This suggests that older fish produce larger eggs that are hatched during the period of peak upwelling in Central Baja and that the smaller eggs from younger fish hatch after the normal peak of upwelling. Thus the alteration of the age structure of the population by fishing could result in a reduction in spawning success. The larvae of younger fish could have a shorter period before starvation would occur. This could be caused by their lesser caloric reserves or a higher metabolic rate due to the higher temperatures they would encounter. Hempel (1965) suggests that the above considerations affect the survival of Norwegian herring.

The distribution of Pacific mackerel larvae is considerably wider than that of the eggs. Principal concentrations are often well offshore and are undoubtedly heavily controlled by transport and convergence patterns. Most larvae have been taken off of Central Baja in the region near Punta Eugenia (Figure 4).

Schooling

Schooling behavior in the California Pacific mackerel stock is not well documented in the literature. Sette (1943), in discussing Atlantic mackerel (Scomber scombrus), reported that fish of the year school separately from the rest. Yearlings usually school separately but may join schools of adults, especially when the adults are predominantly 2-year-olds. The adults, age 2+, travel

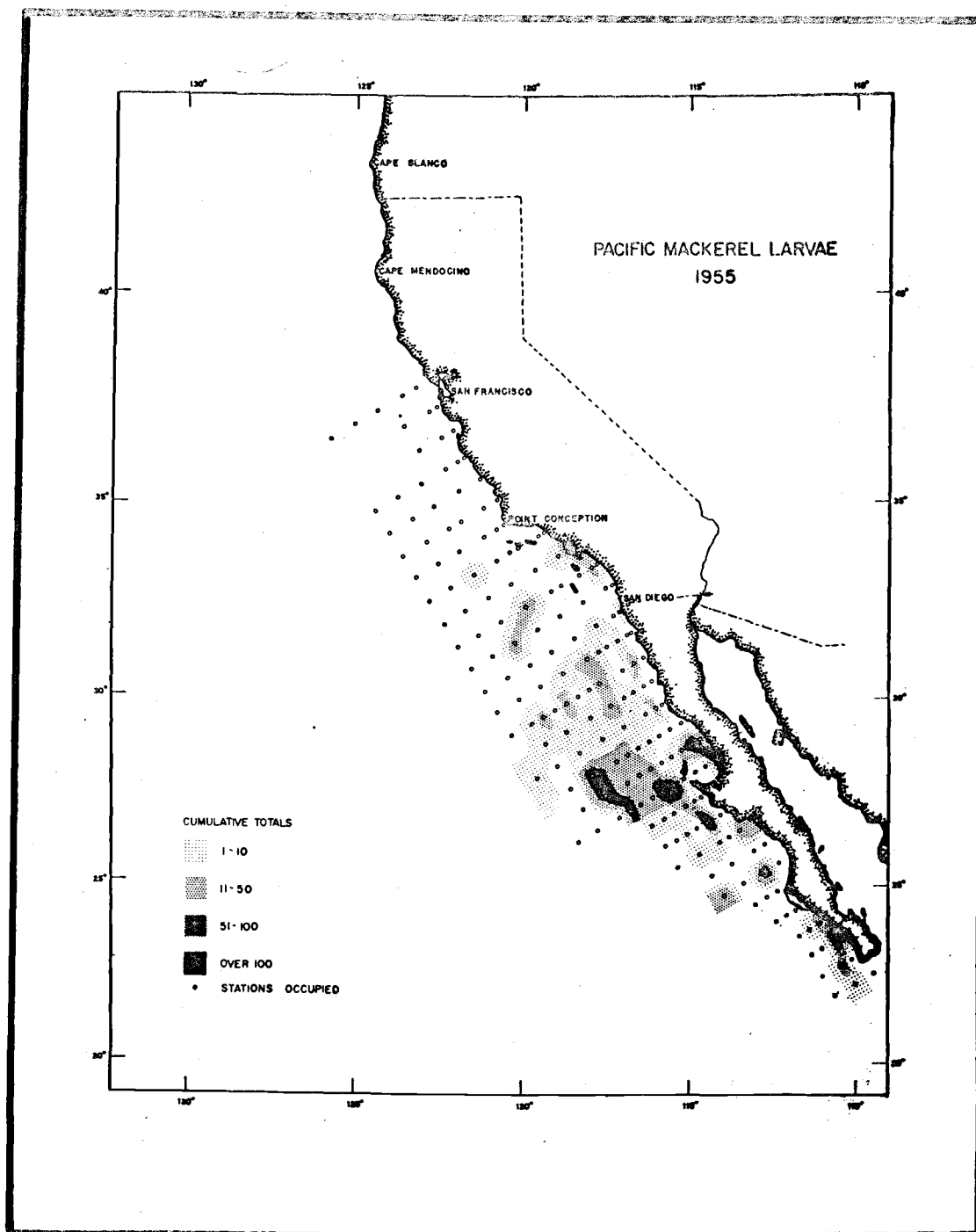


Figure 4 - Distribution and relative abundance of Pacific mackerel larvae in 1955 (fig. 20 of Kramer, 1960)

in mixed schools. Sette attributed the above schooling by age to the fact that the larger, older fish tend to have a higher cruising speed than smaller fish. The age composition of market samples of Pacific mackerel caught off of California suggests that this same pattern is also found in Pacific mackerel. Early management policies favored by members of the canning industry reflected an awareness of this pattern, as they were largely concerned with limiting the catch of young of the year and yearling fish.

It therefore appears that size restrictions could be effective in preventing the capture of young-of-the-year mackerel and to a lesser extent yearlings. Restrictions at sizes or ages larger than this are not feasible in the purse-seine fishery due to the mixed schooling.

POPULATION ESTIMATES

Earlier population estimates based on a Murphy (1966) method cohort analysis were calculated with $M = 0.7$ (Parrish 1974). MacCall (pers. comm.) has shown this mortality rate is probably too large and the population estimates used in the present report were calculated by MacCall, using an instantaneous natural mortality rate of $M = 0.5$ (Figure 5).

The data sources for the cohort analyses were discussed by Blunt and Parrish (1969). The data includes the most extensive, longterm (1939-1969) age composition studies available for any stock in the California Current Region. In addition length

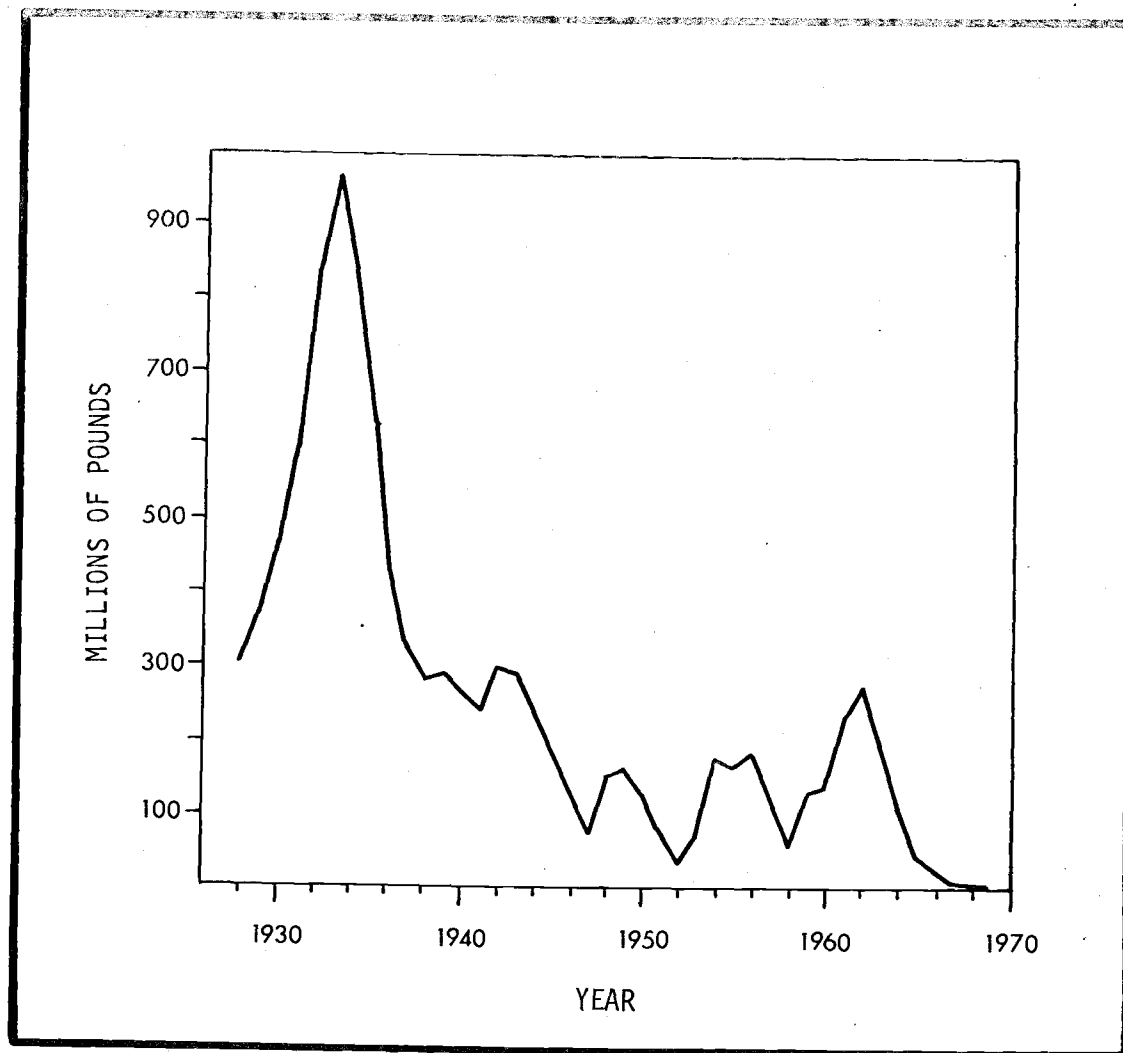


FIGURE 5 Total biomass of the California Current stock of Pacific mackerel (MacCall pers. comm.)

frequencies from market samples are available from 1928-1939. MacCall reconstructed the age structure of the landings from 1928-1938 by separating length frequencies into component normal curves. These curves were determined from age and length data taken during the 1939-1969 period. Landings used for the cohort analysis included the California and Baja California commercial landings and the California sport landings.

The stock described by MacCall's cohort analysis consists of the Pacific mackerel population north of Punta Eugenia, Baja California (Blunt and Parrish 1969).

METHODS

PARAMETER ESTIMATION

The statistical procedures used in this report included extensive use of correlation and regression techniques. The Statistical Interactive Programming System (SIPS) developed and maintained by the Oregon State University Statistics Department (Guthrie, Avery, and Avery 1974) was used almost exclusively for the early analyses. Forward stepwise multiple regression as described by Draper and Smith (1966) was used for analysis including environmental variables. Later analyses included non-linear regressions. These analyses used the Biomedical Computer Program BMDP3R (Dixon 1975). Several of the BMDP3R subroutines were altered for use on a CDC 6500. The program was also altered by the addition of the FORTRAN statements necessary to fit the functions used in the various recruitment models.

Density-dependent recruitment functions

Spawner-recruit functions of several types were fitted to the estimates of recruit biomass (i.e., at age 1) and spawning biomass. The three principal density-dependent functions used were those used by Ricker (1975:282), Beverton and Holt (1957:49), and Cushing (1971). These three functions are shown in Figure 6. The major difference in the three functions is the amount of prerecruitment mortality associated with increasing population density (i.e.,

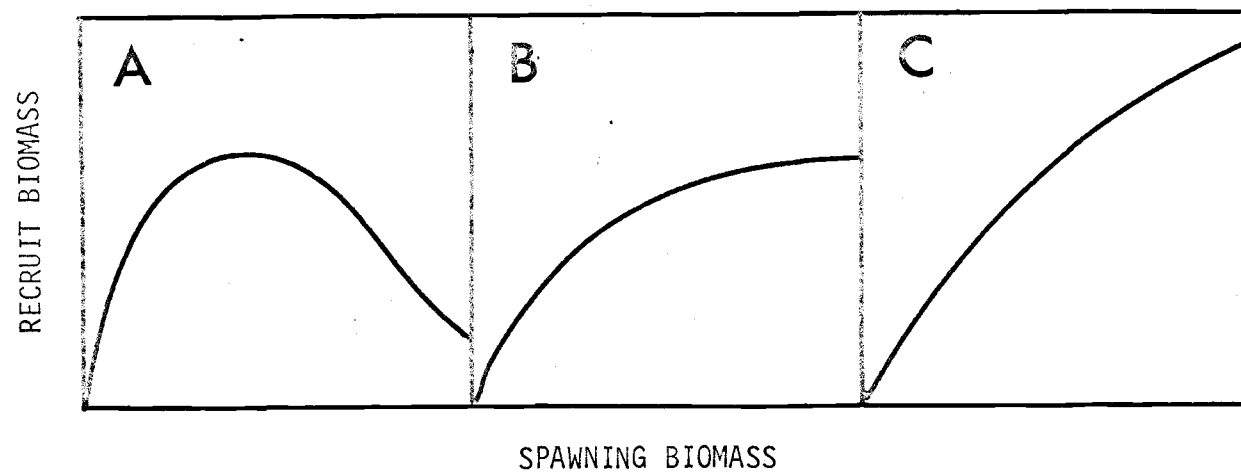


Figure 6 Density-dependent spawner-recruit models; A. Ricker,
B. Beverton and Holt, C. Cushing

compensatory mortality). The Ricker function predicts that recruitment increases to a maximum at some moderate spawning biomass level and then decreases to low recruitment at high spawning biomass levels. The Beverton and Holt function predicts that recruitment increases to an asymptote as spawning biomass increases. The Cushing function predicts that recruitment continues to increase with increasing spawning biomass, however at a continually diminishing rate.

Clark (1974) has suggested that depensatory mortality should occur at low biomass levels in pelagic schooling fishes. This increase in mortality rate at low biomass levels would be caused by a decrease in the average school size, which would result in a reduction in the survival value of schooling. Two spawner-recruit functions were used to determine if Clark's hypothesis could be used to improve the spawner-recruit relationship in a stock that had suffered recruitment failure. These two spawner-recruit functions were made by including a depensatory term in the Ricker and Cushing spawner-recruit functions.

The five spawner-recruit functions were fitted with linear regressions, with log transformed variables, and nonlinear regressions. The equations for the five models and the regression variables used to fit the linear regressions are listed in Table 1. The R^2 and F values for the transformed linear regressions were calculated by the SIPS program. These values for the linear and

TABLE 1. REGRESSION VARIABLES FOR SPAWNER-RECRUIT FUNCTIONS

NAME	FUNCTION	LINEAR REGRESSION VARIABLES	
		DEPENDENT	INDEPENDENT
Ricker	$R = b_1 P e^{-b_2 P}$	$\ln(R/P)$	P
Cushing	$R = b_1 P^{b_2}$	$\ln(R)$	$\ln(P)$
Beverton and Holt	$R = \frac{P}{b_1 + b_2/P}$	P/R	P
Clark-Ricker	$R = b_1 P e^{-b_2 P} e^{-b_3/P}$	$\ln(R/P)$	$P, 1/P$
Clark-Cushing	$R = b_1 P^{b_2} e^{-b_3/P}$	$\ln(R)$	$\ln(P), 1/P$

where

R = Recruit biomass

P = Parent biomass

b_1 = Density independent coefficient

b_2 = Compensatory, density dependent coefficient

b_3 = Depensatory, density dependent coefficient

curvilinear models were calculated by a short FORTRAN program that calculates the total sum of squares, corrected for the mean, and the residual sum of squares for the regression models.

Environmental variables

The environmental data used in this study are available primarily as monthly means. Environmental factors, such as Bakun's (1973) upwelling indices or sea surface temperature at Scripps Pier, therefore consisted of 12 individual variables. These variables are not completely independent. For example sea surface temperatures from adjacent months are obviously highly correlated. In fact seasonal patterns, in the association between the monthly means and recruitment, occurred in most of the environmental factors. The lack of independence between the monthly means was not a necessary prerequisite in the development of recruitment models. The models were developed with stepwise regression, which does not require that all potential variables be completely independent.

The major spawning season for Pacific mackerel is May-July. The monthly means discussed above may cover too small a portion of the spawning season to test the associations between environmental conditions and recruitment. To assess the associations between longer term environmental conditions and recruitment several 3-month combinations were made. The first combination was the mean value for the three main spawning months (May-July). On the hypothesis that conditions immediately prior to spawning should influence

spawning, the second combination was the mean value for April-June. As previously noted there is a marked seasonal difference in the peak of maturity in Pacific mackerel of different ages. It was therefore thought that the age structure of the population would influence the recruitment response to environmental variables. For example a spawning population consisting primarily of age 1 fish, which have a maturity peak in July, would not be able to take advantage of favorable environmental conditions occurring in May. Therefore, linear combinations of the environmental variables from May-July and April-June were made. These linear combinations were prorated by the age composition of the individual year. For example, if the age composition of the spawning biomass in a given year was 50% ages 3+, 20% age 2, and 30% age 1, the prorated variable was 50% of the May value, 20% of the June value, and 30% of the July variable. The same procedure was used for the prorated April-June variables.

The large number of environmental variables analyzed for this study necessitated that some pre-analysis be carried out before multiple regression models were developed. The pre-analysis was accomplished by calculating the correlation coefficient for the relationship between each environmental variable and recruitment. Three different correlations were made for each environmental variable. These three were the correlations with the recruit biomass (i.e., at age 1), the natural log of recruit biomass, and the

natural log of the recruit biomass divided by the spawning biomass. Hereafter the above three will be referred to as R , $\ln(R)$, and $\ln(R/P)$.

Environmental-dependent recruitment functions

Recruitment models incorporating both density and environmental variables were developed with stepwise multiple regression. The on-line statistical system used for stepwise multiple regressions (SIPS) is limited to 50 variables, so it was necessary to reduce the number of potential independent variables. The independent variables used were the previously discussed linear combinations of the spawning months and all other variables with a significant correlation (95% level) with the dependent variable.

In Pacific mackerel the environmental variables were more strongly correlated with recruitment than were the density variables. It was felt that the size of the parent stock must have underlying effects on recruitment as suggested by Clark (Clark and Marr 1955). The fact that recruitment is heavily dependent upon environmental factors does not negate the effects of parent stock size; it merely masks the effects. Therefore the multiple regression models developed included density-variables. The models were developed by adding the density variable to the regression model before the stepwise process was started (i.e. forcing in the density variable before any environmental variables were allowed to enter the regression). This had the effect of adding environmental variables

that best describe recruitment given the fact that a density variable is included in the model. However this is not to say that the multiple regression models describe variation from the density-dependent Ricker or Cushing models.

SIMULATION MODELS

The computer simulation models used in this work were originally written in ALGOL and were run on a CDC 3300 computer. They were later converted to FORTRAN IV and were run on a CDC 6500 computer. Two simulation models were used. The simpler model (ISOE, Appendix I) is a yield-per-recruit model based on the yield equations described by Beverton and Holt (1957) and as revised by Ricker (1975). ISOE calculates the relative yield from a cohort at various combinations of exploitation rate and age at recruitment to the fishery.

The ISOE program calculates yield matrices for 1000 weight units of recruits. The matrices are output with the exploitation rates (and instantaneous fishing mortality rates) on one axis and age at recruitment on the other axis. The program is run with user supplied increments of exploitation rate and the instantaneous fishing mortality rates are calculated with an iterative solution based on Newton's method. User supplied input includes the maximum age of the species, the proportion spawning by age group, the Bertalanffy growth equation constants, the length-weight equation constants, the minimum and maximum ages at recruitment, and the exploitation rates for which the simulation is run.

The second simulation model (QUOTAE, Appendix II) was developed to simulate the Pacific mackerel population under a quota system similar to the present California regulations governing the fishery. QUOTAE is a dynamic pool model and includes a spawner-recruit function. This model combines many of the ideas used by Walters (1969) and Allen (1973). QUOTAE calculates the mean yield over a period of years with various combinations of quota proportion and age at recruitment. The quota proportion is defined as a fraction of the stock above some minimum level. The minimum level in the case of the California Pacific mackerel regulations is the spawning biomass level at which a moratorium on commercial fishing comes into effect (i.e., 20 million pounds). In the case of salmon the minimum level might be the minimum escapement.

The program can be run with no minimum biomass level, with a minimum biomass level or with a lower biomass level and an upper biomass level. In the first option the quota proportions are identical to exploitation rates. The second option allows increments of the quota proportion above the minimum biomass level. The third option is patterned after the California regulations and also resembles the approach followed by Allen (1973). As used in the Pacific mackerel simulations the third option would have a lower biomass level of 20 million pounds, a lower quota proportion of 0.2, an upper biomass level of 40 million pounds, and an upper quota proportion that is varied to determine the yields under different quota proportions.

In fisheries where the estimates of recruit biomass are measured at essentially the same time as those of spawning biomass the spawner-recruit curve can be used as an excess production curve. This is the case in some salmon fisheries. In most fisheries this is not the case. Recruitment occurs at some intermediate age and each cohort is exploited over a period of years. Thus for most fisheries the shape of the excess production curve is influenced by both the exploitation rate and the age at recruitment. If environmental factors cause considerable variation from a spawner-recruit function the surplus production curve will also show considerable variation. The QUOTAE model can be used to evaluate the yields under the various surplus production curves resulting from different management policies. This includes policies based on equilibrium yield that use a density-dependent spawner-recruit function. It also allows assessment of yields under a recruitment function that includes both environmental and density-dependent factors. In the latter case the model can be either deterministic or stochastic.

Biological input to the model included growth and proportion spawning by age group, a recruitment function, and natural mortality. Annual growth and growth to capture were the growth proportions calculated with the ISOE program. These calculations were made with the Bertalanffy and length-weight equations presented by Knaggs and Parrish (1973). The proportion spawning by age group was the data reported earlier and the proportion of age 1 spawners

was density-dependent. The natural mortality and fishing mortalities were not age specific and an instantaneous natural mortality of $M = 0.5$ was used in all simulations. Spawner-recruit functions used in the simulations will be presented later and they included density-dependent functions and density-environmental-dependent functions. In several of the environmental-dependent recruitment functions the response to the environmental variables is determined by the age structure of the spawning biomass.

The normal output of QUOTAE consists of yield matrices for the mean yield over the period of the simulation and the yield in the last year of the simulation. The yield in the last year of the simulation is used for equilibrium recruitment functions. Output options include the output of annual spawning biomass, total biomass, recruitment, and yield for each age at recruitment and upper quota proportion. Control card options include the following:

1. Alteration of the quota levels and proportions used to calculate the annual quota.
2. The quota can be based on either the spawning biomass, total biomass, or the combined biomass of one-year-olds and two-year-olds.
3. A percentage catch of undersized fish can be set.
4. The proportion of a year class that spawns can be density-dependent.
5. The environmental variables used in the recruitment

function can be weighed by the proportion of the biomass that spawns during different periods of time.

For specific details the reader is referred to Appendix II.

RESULTS AND DISCUSSION

ASSOCIATIONS BETWEEN RECRUITMENT AND ENVIRONMENTAL FACTORS

Sea surface temperature

Off of southern California, warm sea surface temperature during the spawning season was found to be associated with good recruitment in Pacific mackerel. This pattern was seen in the Marsden Square quadrant off of southern California, 120(2), and at Scripps Pier (Figure 7). The sea surface temperature off Baja California, Marsden Square quadrant 84(3), did not show this relationship (Figure 7). After the correlations were run it was found that the 84(3) quadrant contained observations from the Gulf of California and this undoubtedly biased the data from this quadrant.

The generally expected relationship between sea surface temperature (SST) and the number of recruits per spawner is a dome-shaped curve (Ricker 1975:276). The number of recruits per spawner should rise to a maximum at some optimum temperature and then decline to lower levels as temperature continues to increase. Lett et al. (1975) have suggested that egg production in Atlantic cod from the Gulf St. Lawrence shows this relationship with temperature. The above pattern would be expected to occur in the center of the species' geographical range. The California stock of Pacific mackerel is on the northern, cold-water edge of the range of the species. The fact that upwelling is most intensive during the spawning season of Pacific mackerel also contributes to depressing SST. Therefore the dome-shaped relationship

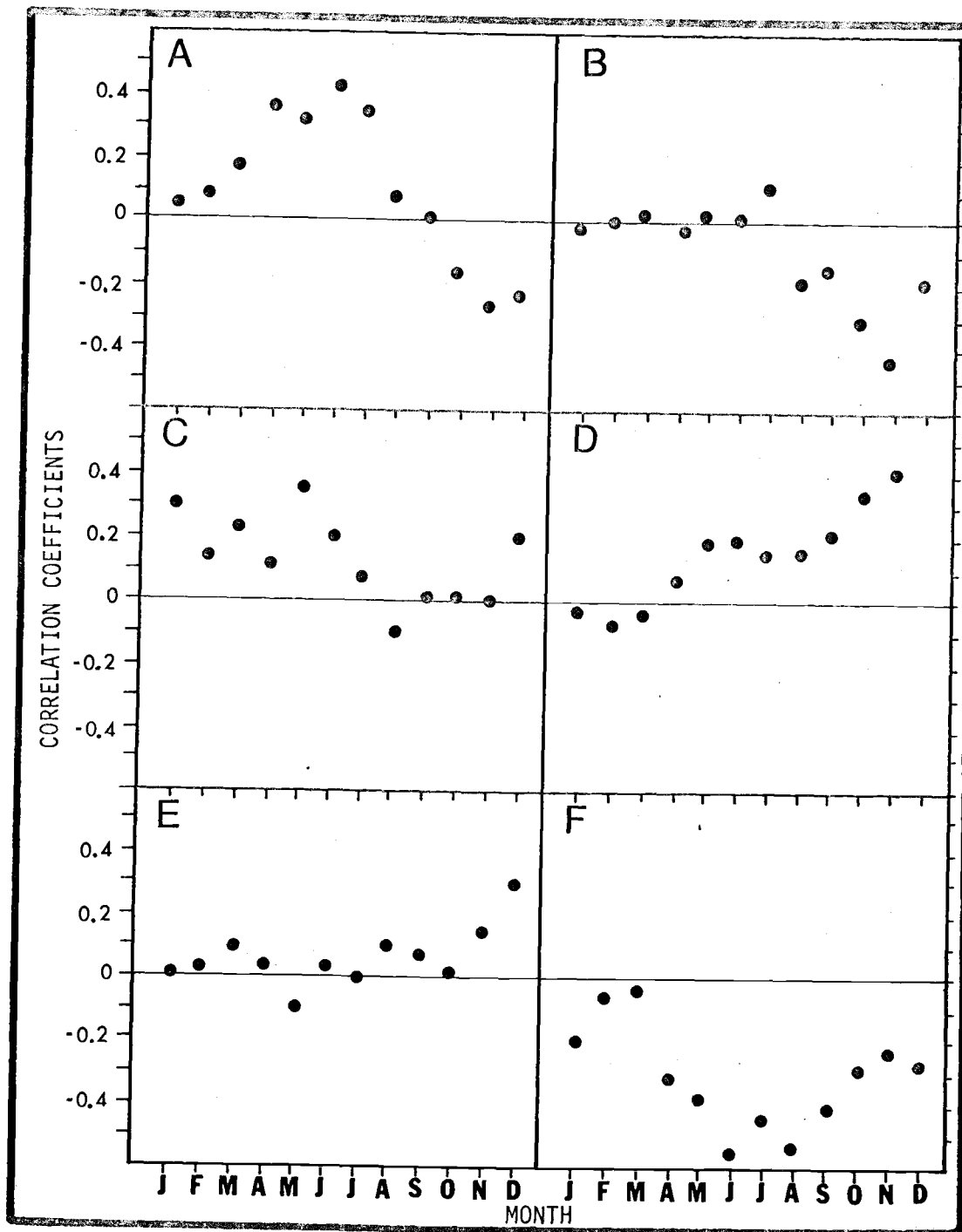


Figure 7 - Correlations of $\ln(R)$ with monthly environmental factors; A. SST in Marsden square 120(2), B. SST in Marsden square 84(3), C. SST at Scripps Pier, D. Sea level differences from Saur (1973), E. Sea level barometric pressure at San Diego, F. Sea level at La Jolla

between SST and the number of recruits per spawner should not be expected to hold for the California stock of Pacific mackerel because the SST does not get high enough to depress recruitment. To approximate this relationship a quadratic multiple regression of $\ln(R/P)$ vs T and T^2 was calculated (where T = prorated April-June sea surface temperature ($^{\circ}\text{C}$) in Marsden Square 120(2)). The first order value of temperature is the first variable to enter, with an r^2 of 0.2611 ($F = 12.72^{**}$ with 36 df). The entering of the second order term is not significant and the r^2 is only increased to 0.2613. The hypothesis that the relationship between $\ln(R/P)$ and SST is quadratic must therefore be rejected for the range of SST observed in Marsden Square 120(2). The first order regression equation is significant at the 99% level.

$$\ln(R/P) = -13.527 + .78815 T$$

This model suggests that warm surface waters are positively associated with good spawning success; however, the relationship shown should only be considered valid with Marsden Square 120(2) sea surface temperatures between 14° and 17.5°C . It should be noted that only 26% of the variation in $\ln(R/P)$ is explained by these data.

Sea level and atmospheric pressure

Monthly mean sea level at La Jolla, corrected for atmospheric pressure, and Saur's (1973) sea level differences between San Francisco and Hilo, Hawaii show different correlation patterns with recruitment. There is a statistically significant negative corre-

lation between recruitment in Pacific mackerel and the sea level at La Jolla for the entire April-September spawning season, (Figure 7). Saur's sea level differences do not show a statistically significant correlation with recruitment during the spawning season but do show positive correlation during the late fall (Figure 7). Monthly means of barometric pressure at San Diego show little correlation with $\ln(R)$, (Figure 7).

Wind speed and cloud cover

Wind speeds in both Marsden Squares show a constant negative correlation with $\ln(R)$, (Figure 8). Cloud cover appears to have little association with $\ln(R)$ and with the exception of one month the correlations are not significant at the 95% level, (Figure 8).

Ekman and total transport

Associations between $\ln(R)$ and transport data tended to show higher correlations than $\ln(R)$ and Marsden Square or shore-based data sets. Data from 30°N tended to be considerably better correlated with $\ln(R)$ than data from 33°N and slightly better than data from 27°N. This is consistent with the observed center of larval distribution (Figure 4).

Bakun's (1973) upwelling indices at 30°N, positive offshore, show spring and fall peaks in association with $\ln(R)$, (Figure 9). Meridional Ekman transport at 30°N shows to a lesser extent the same spring and fall peaks as Bakun's upwelling indices. Values for

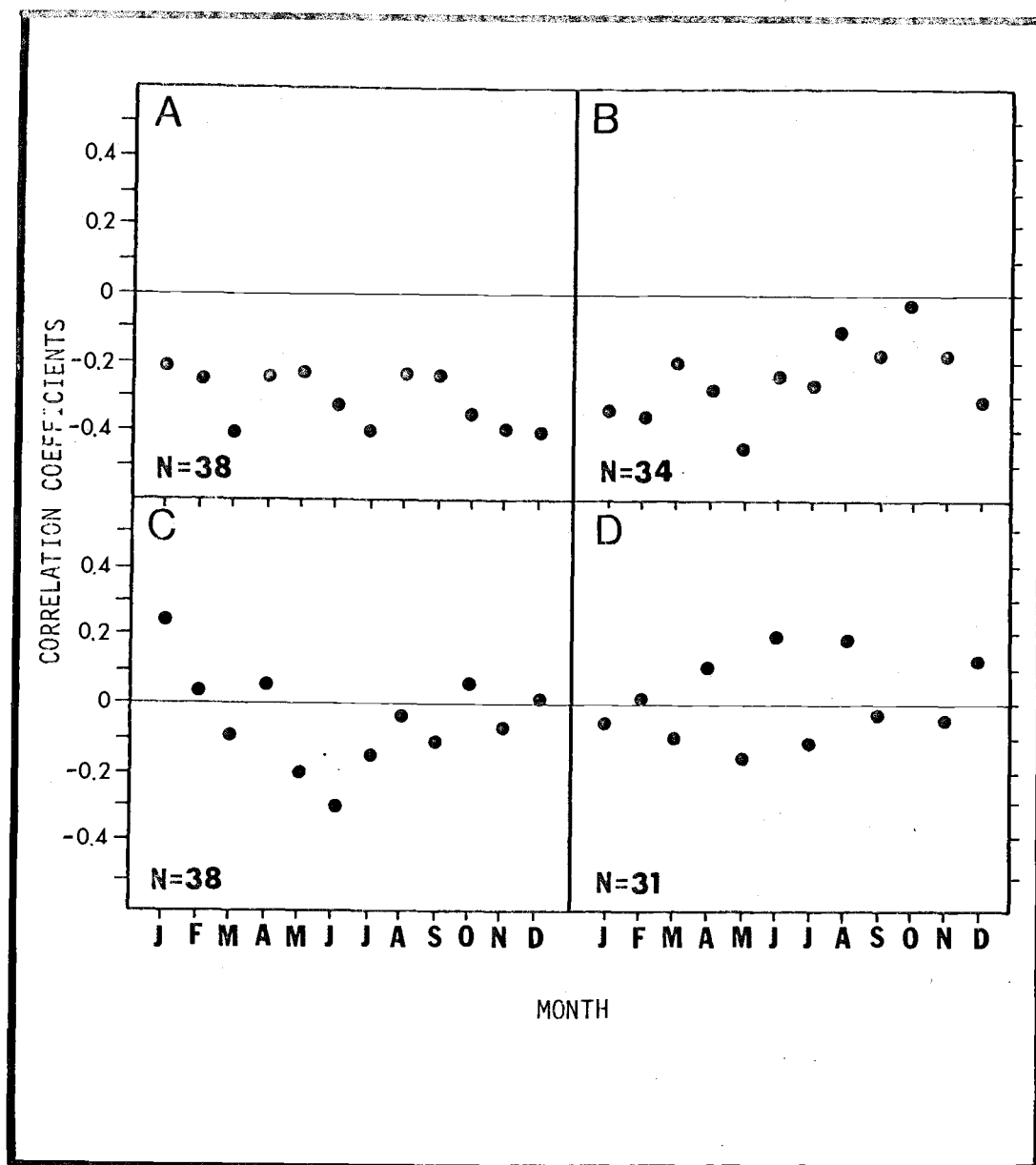


Figure 8 - Correlations of $\ln(R)$ with monthly environmental factors; A. Wind speed in Marsden square 120(2), B. Wind speed in Marsden square 84(3), C. Cloud cover in Marsden square 120(2), D. Cloud cover in Marsden square 84(3).

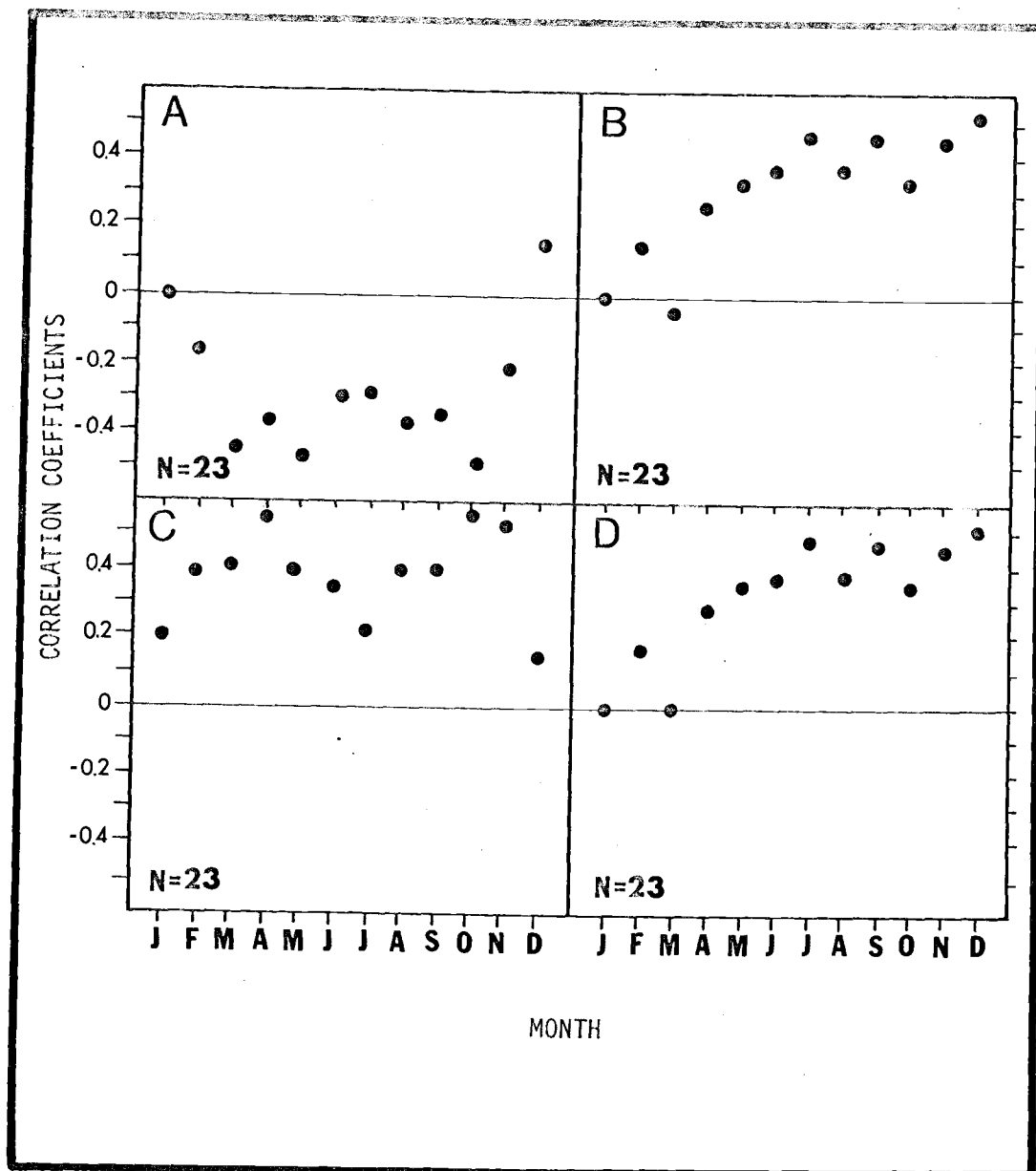


Figure 9 - Correlations of $\ln(R)$ with monthly environmental factors; A. Meridional Ekman transport at 30°N; B. Meridional total transport at 30°N; C. Bakun's (1973) upwelling indices at 30°N; D. Divergence of Ekman transport at 30°N.

meridional Ekman transport were calculated with negative values southward, which accounts for the difference in the sign of the correlation coefficients between the upwelling indices and meridional Ekman transport. There is a positive correlation between $\ln(R)$ and the upwelling indices. This relationship is conceptually satisfying in that increased plankton production resulting from upwelling should be beneficial to larval fishes. It is also noteworthy that the peak of spawning in Pacific mackerel is the same as the peak of upwelling off central Baja (i.e., May-June).

Meridional total transport shows significant, positive correlation with $\ln(R)$ during the end and after the spawning season (Figure 9). The divergence of Ekman transport shows essentially the same monthly correlation pattern as total meridional transport. Total meridional transport and the divergence of Ekman transport at 30°N (wind stress curl) are atypical for the California Current region in that the values are negative. Bakun and Nelson (in press) have shown that negative wind stress curl (convergence), which is characteristic of the offshore region, extends toward the coast in the region just north of Punta Eugenia. They point out that the patterns of negative and positive wind stress curl suggest separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Punta Eugenia (Figure 10). They also note that ship-drift data in the region of negative wind stress curl tend to confirm this hypothesis in that a poleward component is lacking

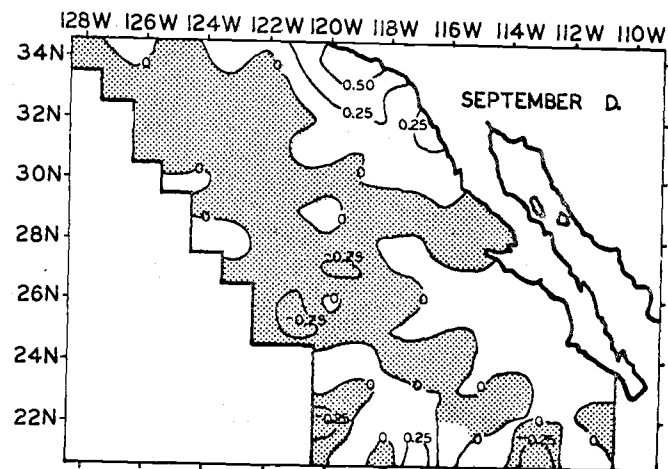
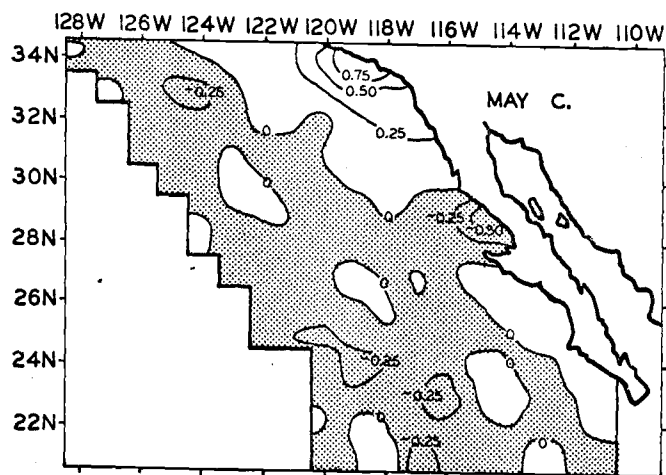
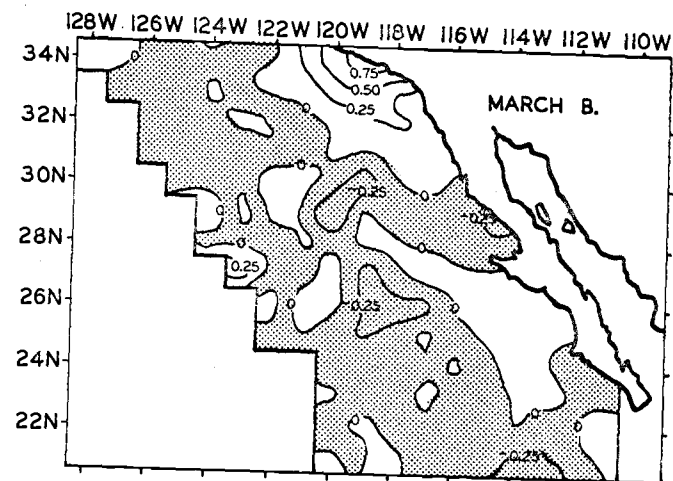
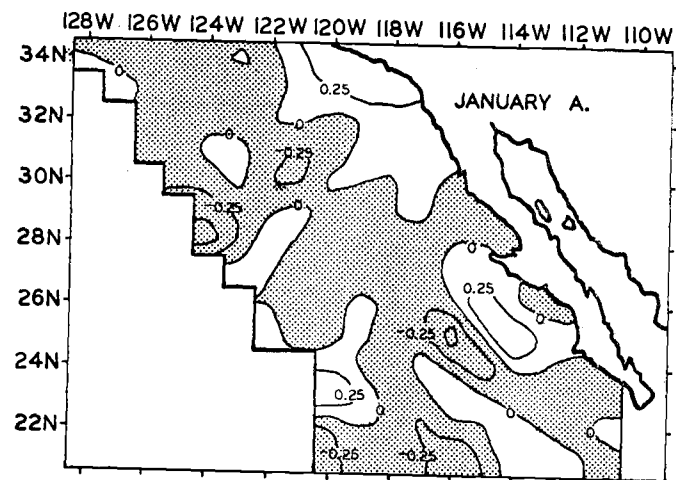


Figure 10 Wind stress curl patterns off of Southern California and Baja California (Bakun and Nelson In Press)

during the fall when the relaxation of upwelling would favor surfacing of a coastal counter current.

Linear combinations of spawning months

Several combinations and prorations of the spawning months resulted in larger correlation with recruitment ($\ln(R)$) than did the individual months (Table 2). Some of this increased correlation may have been fortuitous. However, it is conceptually satisfying that environmental conditions over the entire spawning season are better correlated with recruitment than conditions occurring in any one month. I feel that it is noteworthy that the environmental variable found to have the highest correlation with recruitment is one with very rich biological implications. This variable, April-June upwelling indices at 30°N prorated by the age composition of the spawning biomass, had a correlation coefficient of 0.713 with $\ln(R)$. Over 50 percent of the variation in $\ln(R)$ is explained by this variable. The high correlation with this variable suggests that recruitment is increased if there is upwelling just prior to and during the early part of the spawning season. It also implies that changes in age structure, and therefore time of peak spawning, can alter the response to a given upwelling pattern. It should also be noted that prorating the May-July upwelling indices by the age composition reduced the correlation with $\ln(R)$ to 0.319. The implications are that upwelling a month prior to peak spawning results in greatly increased reproductive success and that upwelling during peak

TABLE 2. CORRELATION COEFFICIENTS OF LINEAR
COMBINATIONS OF MONTHLY VALUES OF
ENVIRONMENTAL VARIABLES WITH $\ln(R)$

Variable	N	May-July Mean	Prorated [#] May-July	April-June Mean	Prorated [#] April-June
SPIER	41	.270	.416**	.276	.255
BARP	41	.030	-.165	-.007	-.059
SSTC	38	.434**	.432**	.432**	.392*
WINDC	38	-.364*	-.380*	-.289	-.306
SLLJ	41	-.542**	-.391**	-.514**	-.392**
SLEV	41	-.509**	-.348*	-.509**	-.366*
UP	23	.458**	.319	.575**	.713**
ODI	23	.528**	.610**	.486*	.584**

- SPIER - Sea surface temperature at La Jolla
 BARP - Barometric pressure at San Diego
 SSTC - Sea surface temperature, Marsden Square quadrant 120(2)
 WINDC - Wind speed, Marsden Square quadrant 120(2)
 SLLJ - Uncorrected sea level height at La Jolla
 SLEV - Sea level height at La Jolla corrected for atmospheric pressure
 UP - Bakun's (1973) upwelling index at 30°N
 ODI - Bakun's (pers. comm.) offshore divergence index at 30°N (divergence of Ekman transport).
 * - Significant at 95% level
 ** - Significant at the 99% level
 # - Variables were prorated as described on page 27

spawning does not significantly increase reproductive success. The above is in agreement with field observations for the northern anchovy, which suggest that storms disperse chlorophyll maximum layers that are necessary for survival of first-feeding anchovy larvae (Lasker 1975).

RECRUITMENT FUNCTIONS

Density-dependent recruitment functions

Spawner-recruit functions were calculated with both linear and nonlinear regression procedures. The linear regression models were fitted with log transformed variables and will hereafter be referred to as transformed models. The exponentiated versions of the transformed models will be referred to as the linear models. Transformed models for the period of 1928-1968 were significant at the 99% level for the Cushing function but the Ricker and Beverton and Holt functions were not significant even at the 95% level (Table 3). None of the linear models are significant at the 95% level. The linear Cushing and Beverton and Holt models had a larger sum of squares than the total sum of squares corrected for the mean. This implies that the linear Cushing and Beverton and Holt models provide significantly worse estimates of recruitment than does mean recruitment.

The nonlinear (BMDP3R) Ricker and Cushing functions are both significant at the 99% level (Table 3). The addition of a depensatory term to the Ricker and Cushing functions only slightly increased the

TABLE 3. DENSITY-DEPENDENT SPAWNER-RECRUIT FUNCTIONS

NAME	FUNCTION	R ²	F	DF
Cushing transformed	$\ln(R) = 2.0948 + 0.72888 \ln(P)$	0.297	16.49**	1,39
Cushing linear	$R = 8.1238 P^{0.72888}$	-	-	1,39
Cushing nonlinear	$R = 1069.9 P^{0.36187}$	0.166	7.78**	1,39
Beverton and Holt transformed	$P/R = 6.1961 + 0.0000030821 P$	0.002	0.09	1,39
Beverton and Holt linear	$R = \frac{P}{6.1961 + 0.0000030821 P}$	-	-	1,39
Ricker transformed	$\ln(R/P) = -0.67752 - 0.00000214 P$	0.068	2.85	1,39
Ricker linear	$R = 0.50787 P e^{-0.00000214 P}$	0.057	2.31	1,39
Ricker nonlinear	$R = 0.88093 P e^{-0.00000253 P}$	0.236	12.06**	1,39
Clark-Cushing nonlinear	$R = 2435.4 P^{0.29910} e^{-7524.3/P}$	0.170	4.39*	2,38
Clark-Ricker nonlinear	$R = 0.85112 P e^{-0.00000242 P} e^{3501.0/P}$	0.237	5.90**	2,38

R = Recruit biomass in thousands of pounds

P = Parent biomass in thousands of pounds

* = Significant at 95% level

** = Significant at the 99% level

coefficients of determination (R^2); the Clark-Ricker function was significant at the 95% level (Table 3). The Clark-Ricker function converged to a positive coefficient and therefore this model contains two compensatory terms rather than a compensatory term and a depensatory term. The fact that the addition of depensatory terms did not improve the fits of the spawner-recruit functions does not necessarily imply that a depensatory recruitment factor does not exist in Pacific mackerel. The large observed variation in recruitment at low spawning biomass levels would have hindered detection of a depensatory factor and it is possible that depensation would not occur until the spawning biomass reached extremely low levels.

The three Ricker models (Table 3) have very low density-independent coefficients. This suggests that the limiting equilibrium rate of exploitation will be quite low in comparison to other fisheries (Ricker 1975:286). The poor statistical fit of the Ricker models is apparent in the large variation in $\ln(R/P)$ that occurred when the spawning biomass was less than 200 million pounds (Figure 11).

Fitted curves for the linear and nonlinear Ricker and Cushing functions are shown in Figure 12. The curves for the linear functions show considerable similarity in form at spawning biomass levels below 350 million pounds. The nonlinear, BMDP3R, Ricker and Cushing curves also show considerable similarity. It appears that at least for low and moderate spawning biomass levels the way the functions are fitted is more important than which function is used.

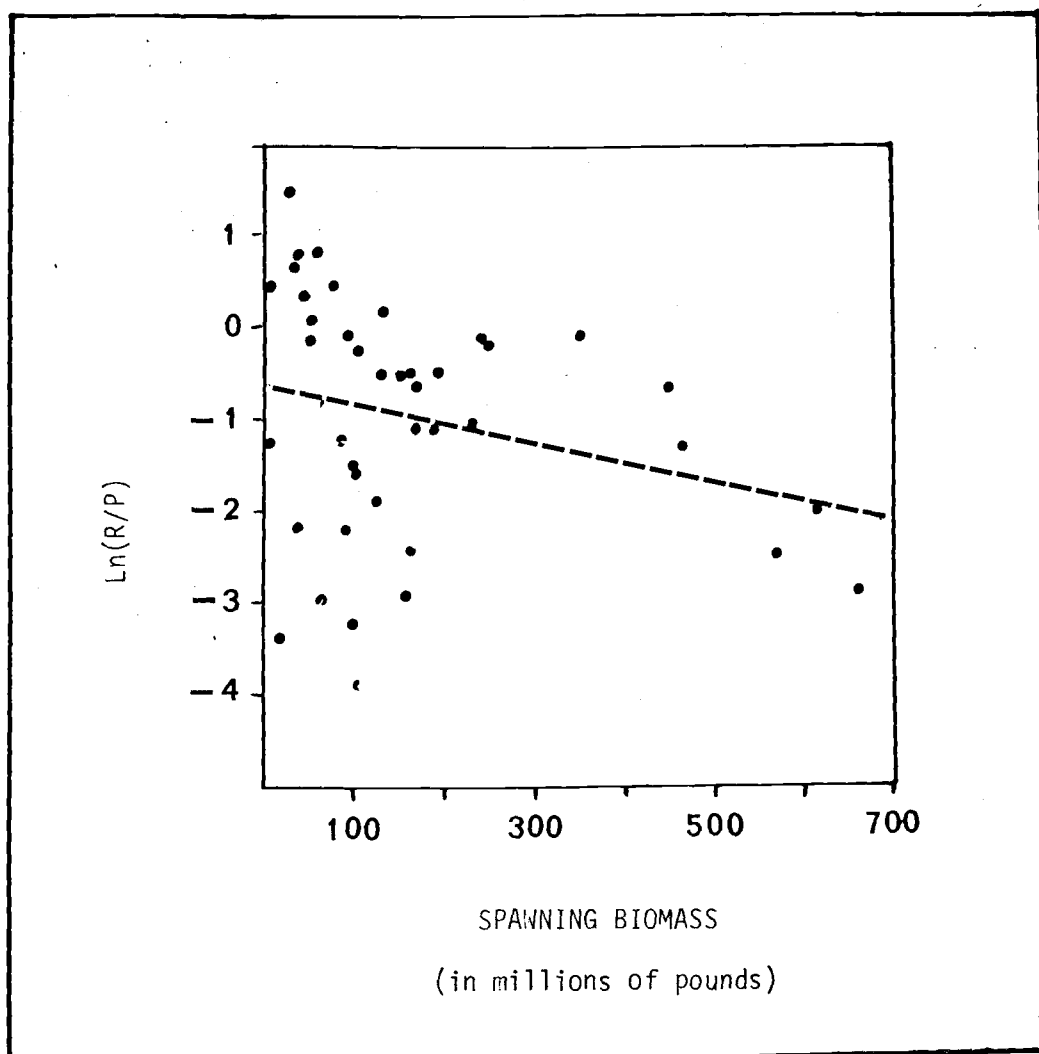


Figure 11 - Natural logarithms of recruit biomass per spawning biomass plotted against spawning biomass (including fitted regression line).

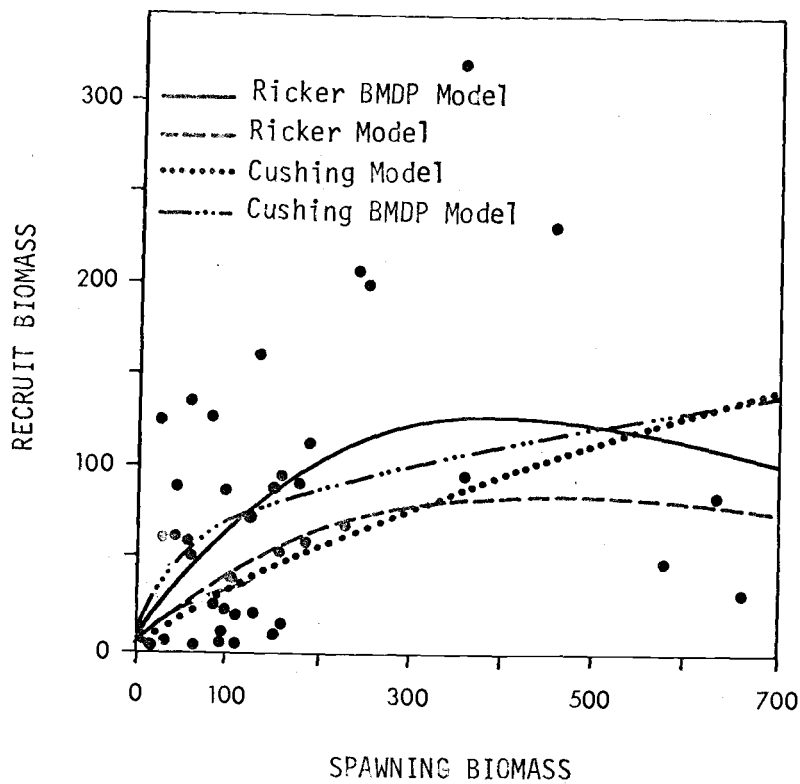


Figure 12 - Ricker and Cushing spawner-recruit models fitted to Pacific mackerel population data. (Values in millions of pounds).

The Cushing and Ricker models above were transferred to spawner resultant-spawner models to show equilibrium points (Figure 13). This transfer was calculated by multiplying the calculated recruitment by a factor that determines the spawning biomass of a cohort that would occur when there was no fishing mortality. This factor (3.845) was calculated by the ISOE program. The resulting spawning biomass per unit weight of recruits calculated with this program assumed a constant (0.26) proportion of maturity of age 1 fish. With the assumption of density-dependent maturity of age 1 fish the spawner resultant spawner relationship would be somewhat more arched than shown in Figure 11 and the equilibrium points would be at a lower spawning biomass.

Environmental-dependent recruitment functions

Recruitment functions incorporating both density-dependent and environmental-dependent factors were developed with forward stepwise multiple regression procedures. This limited the possible recruitment models to functions that are linear or functions that can be transformed to linear functions. It was decided that the use of exponential environmental terms was the most promising as both the Ricker and Cushing spawner-recruit functions can be fitted with linear regression of log transformed terms. This approach has been recommended by Ricker (1975), who suggests that the expected effects of the physical environment are multiplicative rather than additive

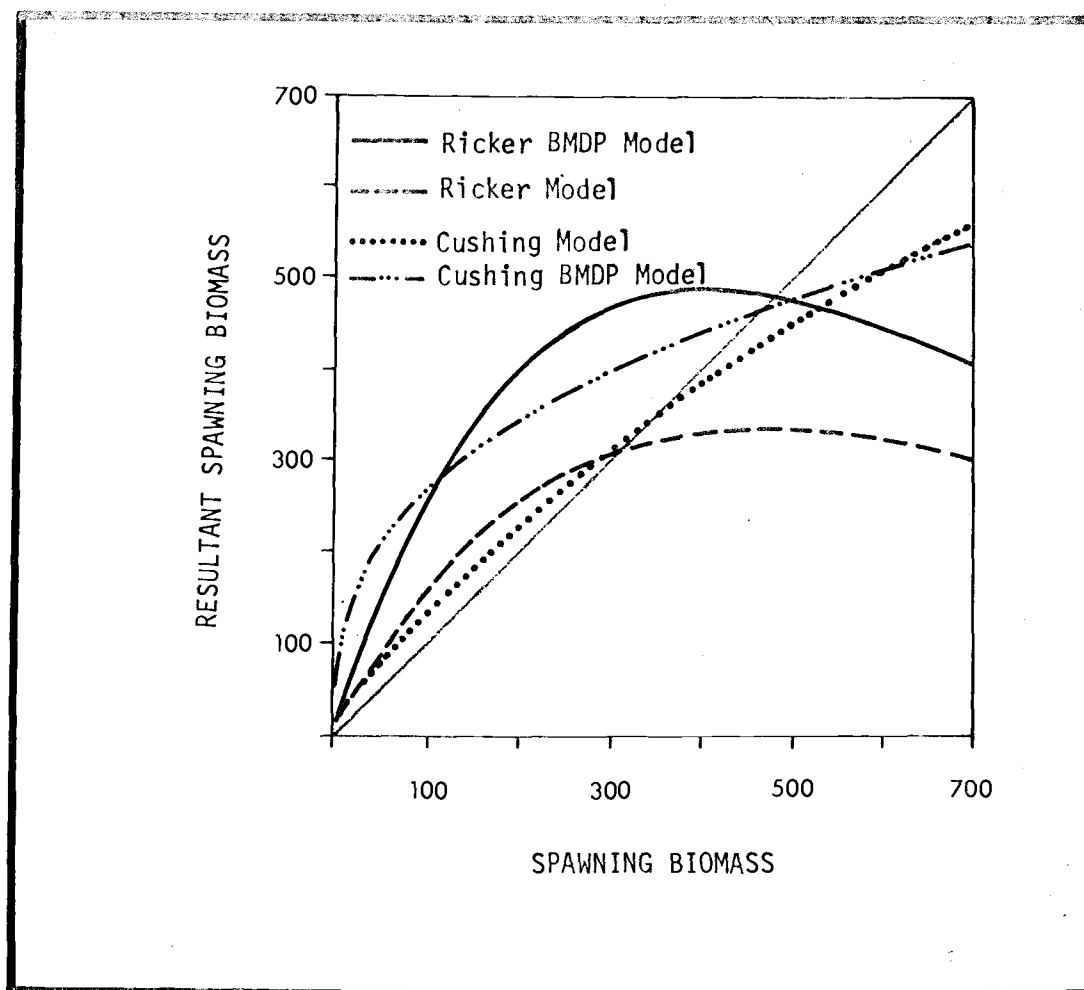


Figure 13 Ricker and Cushing spawner resultant-spawner models (values in millions of lbs)

and therefore logarithms should be used in multiple regressions. Log transformed functions are fitted to the geometric mean rather than the arithmetic mean. When these functions are transformed back to the original form they are biased towards low values. To avoid this bias the parameters of the spawner-recruit functions developed with stepwise multiple regression were computed by regressing the functions with the BMDP3R nonlinear regression program. This program requires a FORTRAN subroutine, which principally consists of the individual functions and the partial derivatives of the parameters of the functions. The subroutine used for all nonlinear regressions is listed in Appendix III.

The stepwise multiple regression models were fitted, as previously described, with the density term assigned as the first variable in the forward stepwise process. The density terms were $\ln(P)$ for the Cushing function and P for the Ricker function. Entering environmental terms were accepted if their entering F values were significant at the 95% level. The exception to this is that the number of variables accepted was limited by the number of observations in each case. Draper and Smith (1966:167) suggest that the number of variables in the fitted model should not exceed one variable for every 5 to 10 observations.

Models were developed over three different time periods. Models developed for the first time period (1931-1968) included the Ricker and Cushing based models fitted with the Marsden Square and

shore-based data sets. A Ricker based model was developed for the same data set for the reduced period of 1931-1960. This model was used to determine if the population decline of the mid-1960's would be predicted with a model that was fitted to data that did not include this population decline. The third set of models included the Ricker and Cushing based models fitted with all environmental data sets (1946-1968).

It was decided to limit the multiple regression models fitted to the 1931-1968 data sets to four independent variables due to the number of observations (38). The four variables were the density term and three environmental terms. The model fitted to the 1931-1960 data sets was not fitted by stepwise multiple regression. This multiple regression model was used for comparative purposes and it was decided that it would include only the density and environmental variables that were in the comparable 1931-1968 model.

The models developed from the 1946-1968 data sets were limited to three independent variables, the density term and two environmental terms due to the smaller number of observations (23). The stepwise multiple regression models based on the Ricker and Cushing functions did not always select the same environmental variables. For example in the 1931-1968 models the Cushing-based model selected the May-July mean sea surface temperature and the Ricker-based model selected the April-June prorated sea surface temperature (SSTC, Table 2). The two variables have very similar correlation coefficients with $\ln(R)$, and R^2 values were essentially the same in both

the Cushing and Ricker based models. Due to the similarity of R^2 values it was decided to incorporate the identical environmental variables in the Cushing and Ricker based models for simplicity.

To avoid confusion in later analysis with the environmental-dependent recruitment functions, the functions will hereafter be referred to by the following names. The functions fitted to the 1931-1968 data sets will be called the Ricker sea level model and the Cushing sea level model. The name refers to the first environmental variable to enter the stepwise regressions. The reduced Ricker sea level model will refer to the function fitted to the reduced 1931-1960 data set. Functions fitted to the 1946-1968 data sets will be called the Ricker transport model and the Cushing transport model.

The five environmental-dependent spawner-recruit functions used in the report are listed in Table 4. The environmental variables that were found to best describe recruitment in Pacific mackerel from 1931-1968 are May-July mean sea level at La Jolla; prorated mean May, June, and July barometric pressure at San Diego; and mean April-June sea surface temperature in Marsden Square quadrant 120(2). The Ricker and Cushing sea level models had very similar R^2 values, 0.587 and 0.597, and the F statistics for these models were approximately three times as large as the critical F value at the 99% significance level (Table 4). The reduced Ricker sea level model

TABLE 4. ENVIRONMENTAL-DEPENDENT SPAWNER-RECRUIT FUNCTIONS

FUNCTION NAME	PERIOD COVERED	R^2	F	Df
Ricker sea level	1931-1968	0.587	11.72**	4,33
$R = 51608Pe^{-0.00000353} P_e^{-2.5004} SLEV$ $e^{-0.25594} BARP e^{0.53309} SSTC$				
Cushing sea level	1931-1968	0.597	12.22**	4,33
$R = 100850000P^{0.095703} e^{-2.7680} SLEV$ $e^{-0.09858} BARP e^{0.65528} SSTC$				
Reduced Ricker sea level	1931-1960	0.517	6.68**	4,25
$R = 4214.2Pe^{-0.00000351} P_e^{-2.1837} SLEV$ $e^{-0.19759} BARP e^{0.51148} SSTC$				
Ricker transport	1946-1968	0.756	19.59**	3,19
$R = 0.97815Pe^{-0.0000377} P_e^{0.020787} UP$ $e^{0.0039065} ODI$				
Cushing transport	1946-1968	0.676	13.31**	3,19
$R = 43577000P^{-0.84881} e^{0.02350} UP$ $e^{0.00469} ODI$				

R - Recruit biomass at age 1 in thousands of pounds

P - Parent spawning biomass in thousands of pounds

SLEV - Mean May-July sea level at La Jolla, California in feet (corrected for atmospheric pressure)

BARP - Sea level barometric pressure at San Diego. May, June and July mean pressure prorated by the age composition of the spawning biomass (in millibars minus 1000 millibars)

SSTC - Mean April-June sea surface temperature in Marsden square quadrant 120(2), (in degrees celsius)

UP - Bakun's upwelling index at 30°N. April, May and June indices prorated by the spawning biomass (in M³ per second across 100m width)

ODI - Bakun's (pers. comm.) offshore divergence index at 30°N (Divergence of Ekman transport). April, May, June indices prorated by the spawning biomass (in mm per day positive upwards)

** - Significant at the 99% level

has an R^2 of 0.517. Its F statistic was considerably smaller than the other two sea level models but was still significant at the 99% level.

The Ricker and Cushing transport models include two environmental variables. Both of these variables describe surface transport. The first variable is the April, May and June offshore divergence indices at 30°N prorated by the age composition of the spawning biomass. The Ricker transport model has an R^2 of 0.756 and a F statistic of 19.59 (Table 4). The corresponding statistics for the Cushing transport model are 0.676 and 13.31. The critical F statistic at the 99% level of significance is 5.01.

The predicted recruitment with the Ricker and Cushing sea level models and the observed recruitment are shown in Figure 14A. The same data for the transport models is shown in Figure 14B. The sea level model provides a reasonable description of the general periodicity of recruitment but individual years are not well estimated. The transport model shows a close agreement with the observed recruitment. The only year that is markedly different in observed and predicted recruitment is 1961.

COMPUTER SIMULATIONS

Yield-per-recruit model

Yield-per-recruit isopleths were calculated with instantaneous natural mortality rates (M) of 0.4, 0.5, and 0.6. Bertalanffy growth data used were the previously discussed coefficients from

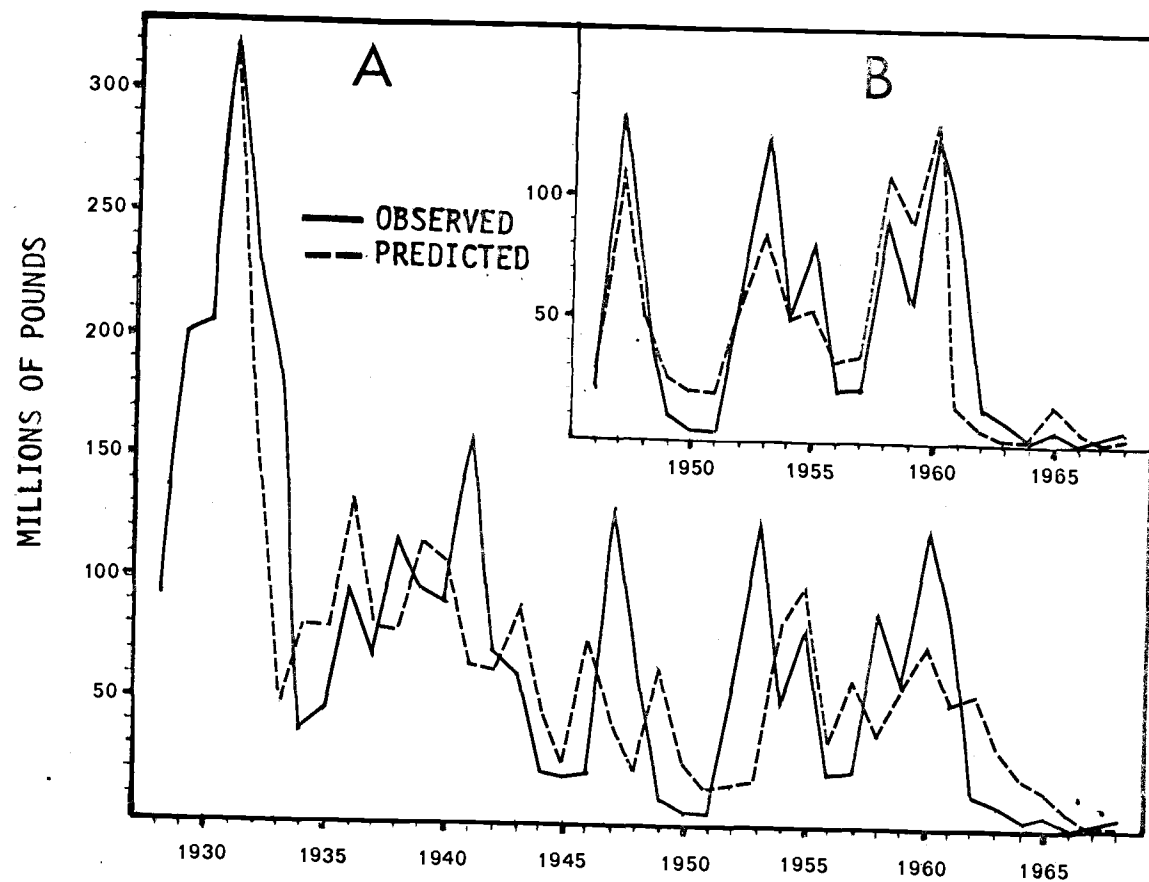


Figure 14 Observed and predicted recruitment of Pacific mackerel
 A. Ricker sea level model, B. Ricker transport model.

Knaggs and Parrish (1973). The program used also calculates matrices of resultant spawning biomass per unit weight of recruits. A generalized version of the program is listed in Appendix I. The proportions of mature fish by age group used for these calculations were 0.26, 0.77, 0.88, and 1.0 for age groups 1, 2, 3, and 4+. Maximum age was 11 (Fitch, 1952).

The maximum yield per unit weight of recruits is dependent upon the choice of natural mortality. The maximum in each case occurred with an age at recruitment of one or less and with $F = 1.0$, the highest instantaneous fishing mortality rate used (Figure 15A). The low age at recruitment for maximum yield is consistent with the species biomass curve with age (Figure 16). This curve shows that when there is no fishing mortality, biomass peaks when the fish are yearlings. Several workers (Walters 1969, Ricker 1975:241) have suggested that the best policy is to harvest each cohort close to the age when biomass loss through mortality balances biomass gain through growth, subject to the constraint that adequate reproduction is maintained.

A fishery operating at the high fishing rates and low age at recruitment necessary to achieve maximum yield-per-recruit in Pacific mackerel results in a situation that produces a minimum spawning biomass from a ton of recruits. Under this fishing strategy, spawning biomass is less than 1/4 of that which occurs with no fishery (Figure 15B).

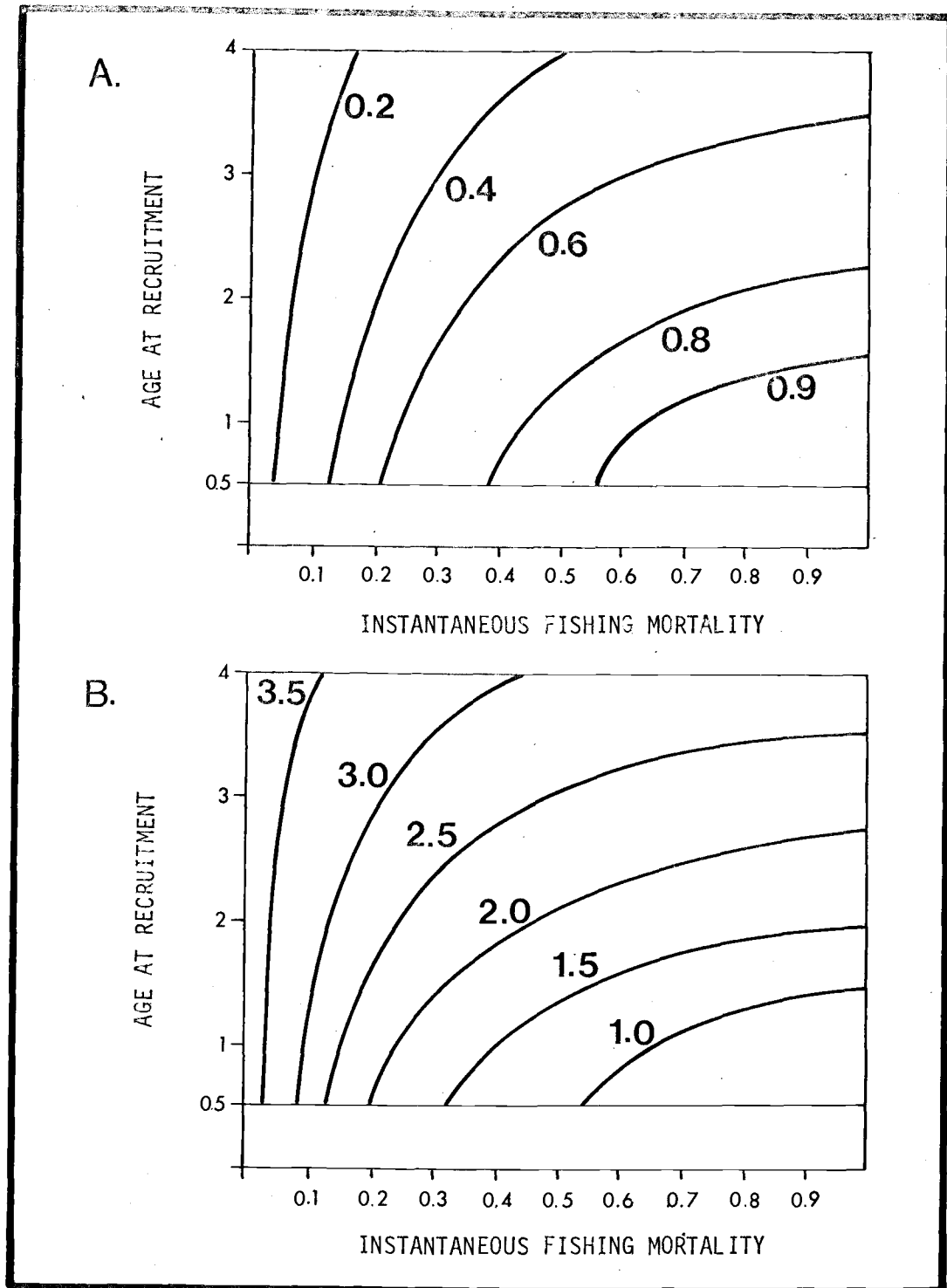


Figure 15 - Isopleth model with $M = 0.5$; A. Yield per unit weight of age 1 recruits; B. Resultant spawning biomass per unit weight of age 1 recruits.

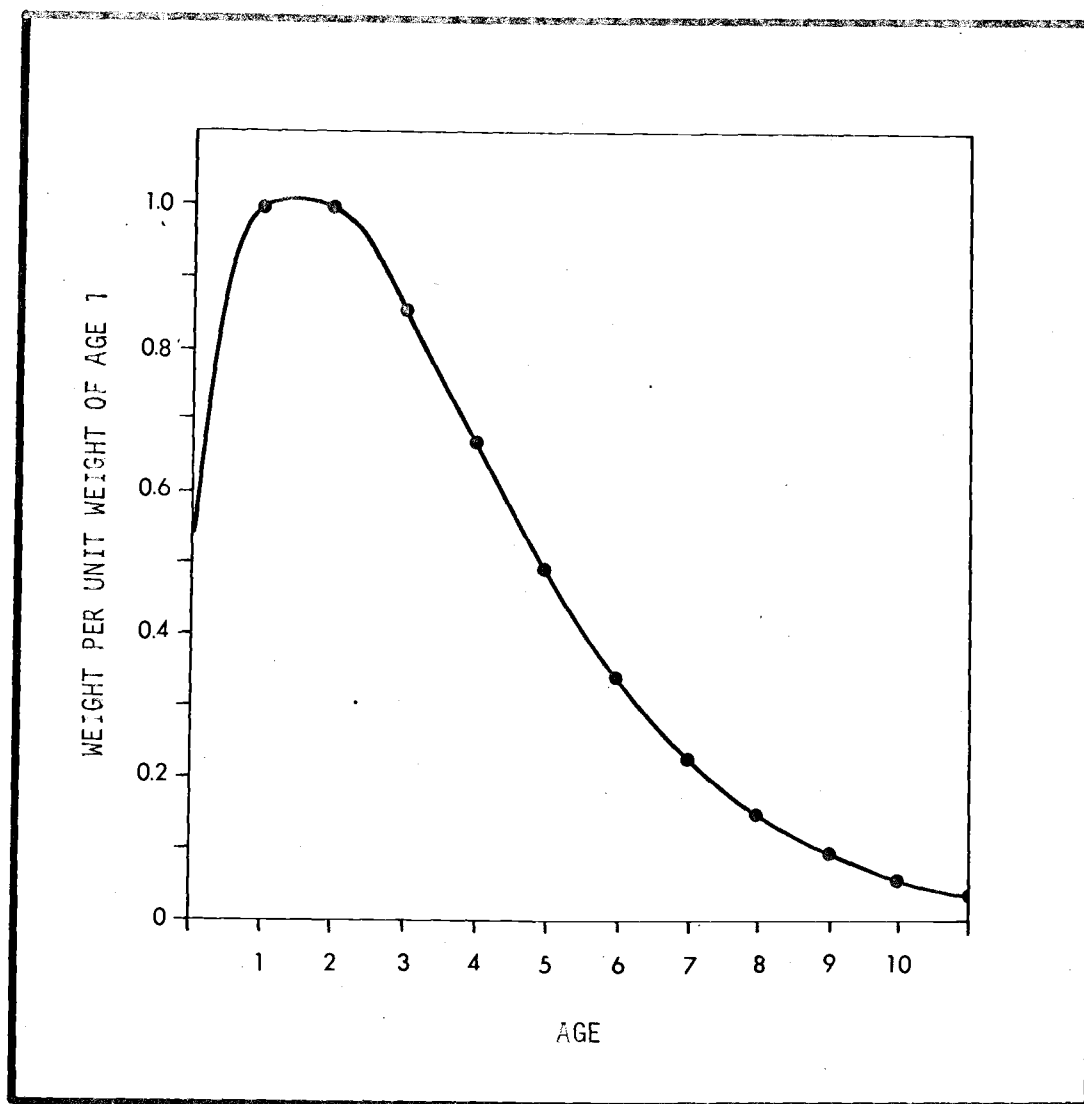


Figure 16 - Pacific mackerel biomass curve with no fishery and $M = 0.5$.

Equilibrium yield simulations with density-dependent recruitment

The QUOTAE model was run with several of the density-dependent recruitment functions previously described. The first series of simulations used the linear and nonlinear regression fits to the Ricker and Cushing spawner-recruit functions (Table 3). In these simulations the quota was based on the total biomass and the quota levels were set at zero. Therefore in these simulations the model calculates the exploitation rates. The second series of simulations was run at various quota levels and the quota was based on the spawning biomass. This series utilized only the Ricker nonlinear regression function. This function was chosen because it has the highest predictive capability. All of the above simulations were run with the 1931 biomass as the starting population. The simulations were run with 5 age at recruitment levels and 20 exploitation rates. The simulations were run for 100 years and the equilibrium yield was taken to be the yield in the 100th year. Simulations with all of the above models had stabilized by the 12th to the 50th year of the simulations. Yields during the 90th to 100th year varied less than 0.001% with each of the above models.

Equilibrium yield isopleths for the Ricker and Cushing recruit-spawner models show the same similarity as that previously described in the spawner-recruit curves (Figure 17). The linear fits to the Ricker function and the Cushing function produce similar yield isopleths and the nonlinear fits also produce similar isopleths.

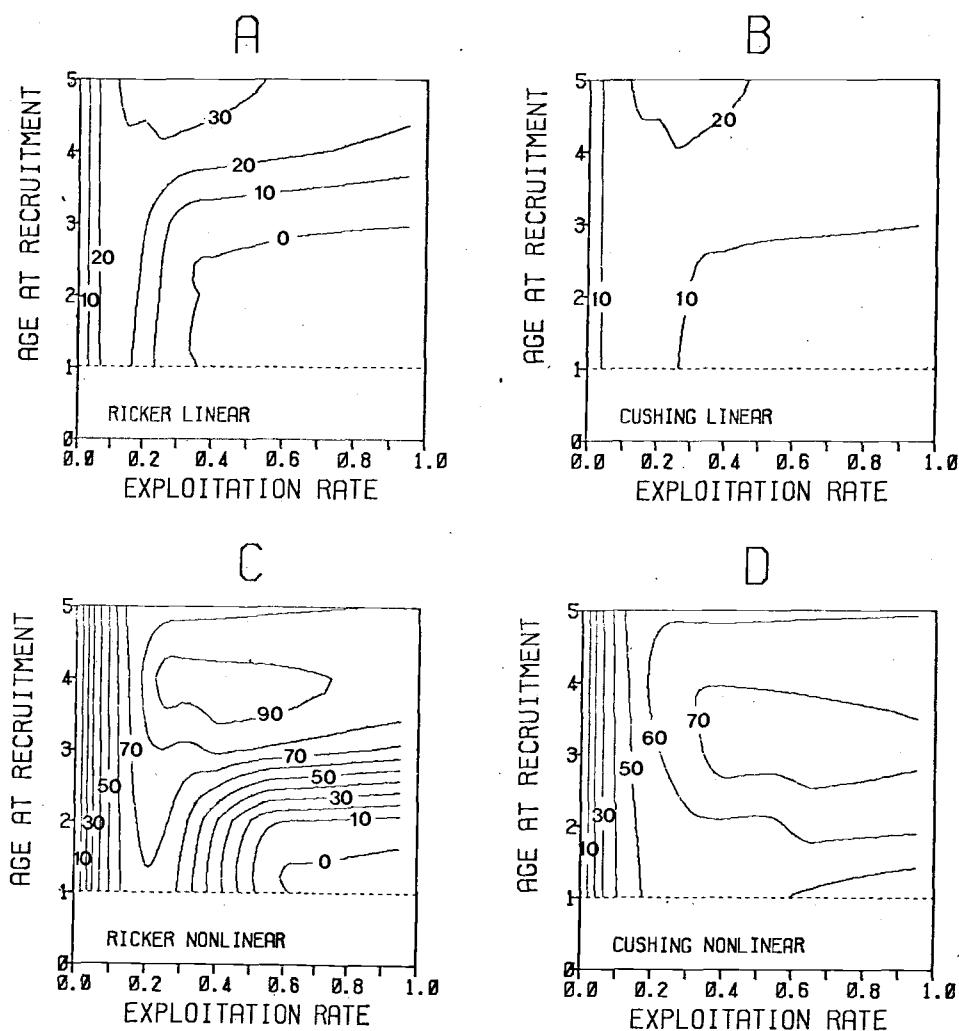


Figure 17 QUOTAE equilibrium yield isopleths with density-dependent spawner-recruit functions (Yield in millions of lbs)

The linear regression fits to the Ricker and Cushing functions have a bias towards low estimates as they are fitted with log transformed variables. This bias is evident in the low equilibrium yields predicted by the isopleths calculated with the linear regression spawner-recruit functions. Average observed yield from 1931 to 1968 was 49 million pounds (22,000 metric tons).

The recruitment functions fitted by linear regression predict that maximum yield will occur with an age at recruitment of above age 4 and at low exploitation rates. Maximum equilibrium yield with an age of recruitment of 1 is with exploitation rates of around 0.15 to 0.3.

The recruitment functions fitted with nonlinear regressions predict that maximum equilibrium yield will occur with an age at recruitment of between 3 and 4. At this age at recruitment and with exploitation rates in excess of about 0.2 the Ricker nonlinear function predicts equilibrium yields above 80 million pounds (36,000 metric tons) and the Cushing nonlinear function predicts yields above 60 to 70 million pounds (27,000 to 32,000 metric tons). High exploitation rates show little reduction in yield at an age of recruitment of 3 to 4. It should be noted that the Ricker functions predict that extinction will occur if the age at recruitment is 1 or lower and the exploitation rate exceeds 0.6. It has been shown that during the population collapse of the late 1960's the exploitation rate on the Pacific mackerel exceeded 0.6 and the age at recruitment was less than age 1 (Parrish, 1974).

Equilibrium yield simulations with four different sets of quota levels show little difference in yields at upper quota proportions below 0.4 (Figure 18). When the upper quota proportions are above 0.5 and the age at recruitment is 1 or 2 the equilibrium yield is markedly depressed in the simulation with the quota levels set at zero (Figure 18A). The maximum equilibrium yield with all of the four sets of quota levels occurs at an age of recruitment of around 4 and with an upper quota proportion of above 0.4.

The present California regulations controlling the Pacific mackerel fishery consist of the quota levels and lower quota proportion as in Figure 18B and an upper quota proportion of 0.3. The age at recruitment during most of the fishery was age 1. This location in the yield isopleth is shown by the symbol X. This series of simulations suggests that, if environmental factors are not considered, the quota levels and quota proportions in the California regulations are properly set from an equilibrium yield philosophy. The simulations suggest that the yields could be increased by enforcing a strict size limit. Maximum equilibrium yield would be impossible with the present purse-seine fishery but could be achieved by a return to the scoop fishery, which could technically be controlled to greatly reduce the catch of fish less than 3 years old.

Yield with environmental-dependent recruitment functions

Two series of simulations were made with the QUOTAE program and environmental-dependent recruitment functions. The first

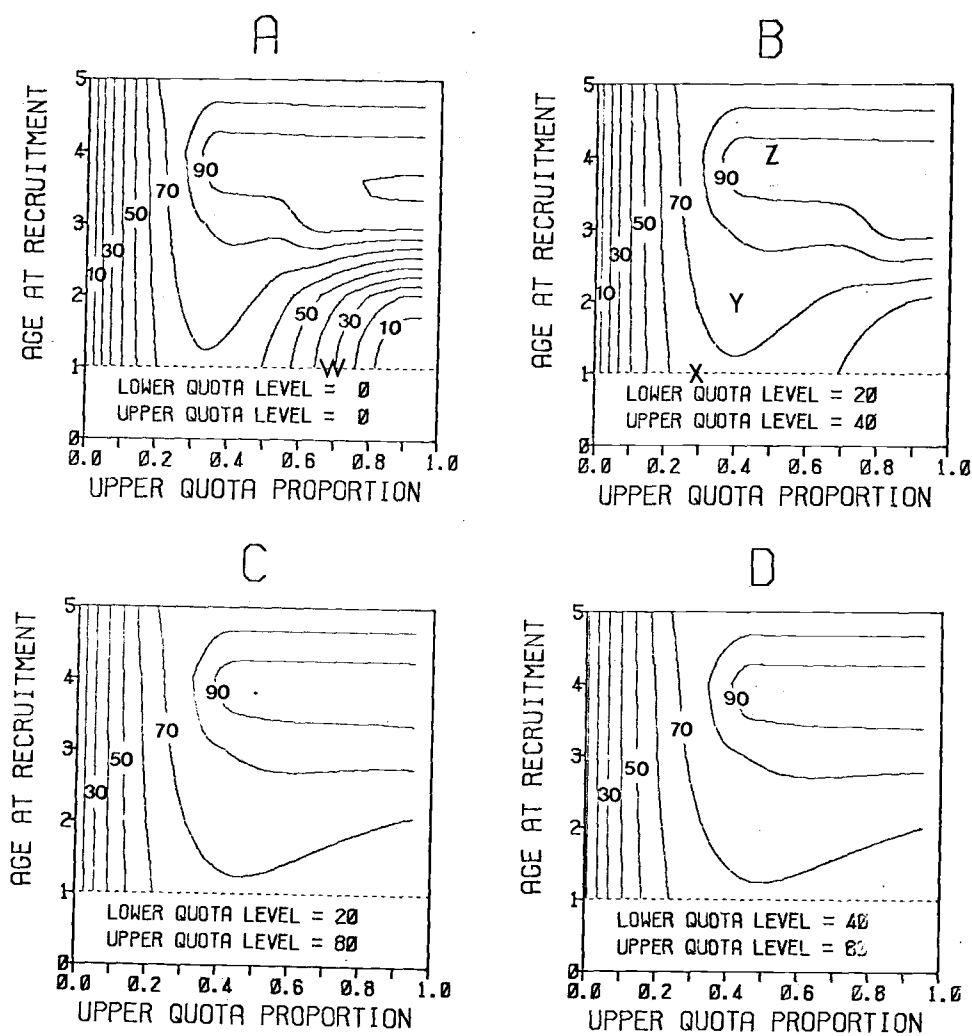


Figure 18 QUOTAE equilibrium yield isopleths, at four different sets of quota levels with the Ricker nonlinear model (Yield in millions of lbs, quota based on spawning biomass)

series utilized the nonlinear Ricker sea level function (Table 4). These simulations started in 1931 with the observed 1931 biomass, by age group, and ran through 1968. The second series used the nonlinear Ricker transport recruitment function, the 1946 starting biomass, and ran through 1968.

The above simulations were run in a manner that differs from the way such simulations are normally run. In most fisheries models environmental variation in recruitment is considered to be a random process (Allen 1973, Walters 1975). Simulations are therefore usually run with a stochastic environmental term. The driving stochastic variable is usually picked from either a distribution with the same mean and variance as the observed environmental variation or from a distribution with a mean of zero and a variance the same as the observed variance from some recruitment function. Variation in recruitment of Pacific mackerel is markedly nonrandom; instead it shows an aperiodic cyclic pattern. This pattern can be readily seen in a time series of the natural log of the number of observed recruits per spawner (Figure 19). Because of the non-randomness of recruitment it was decided that a more realistic assessment of the effects of alternative management policies would be obtained by using the observed environmental data to generate recruitment. For example, the simulations with the nonlinear Ricker transport function were run with the observed April, May and June mean values for the upwelling indices and offshore divergence indices at 30°N.

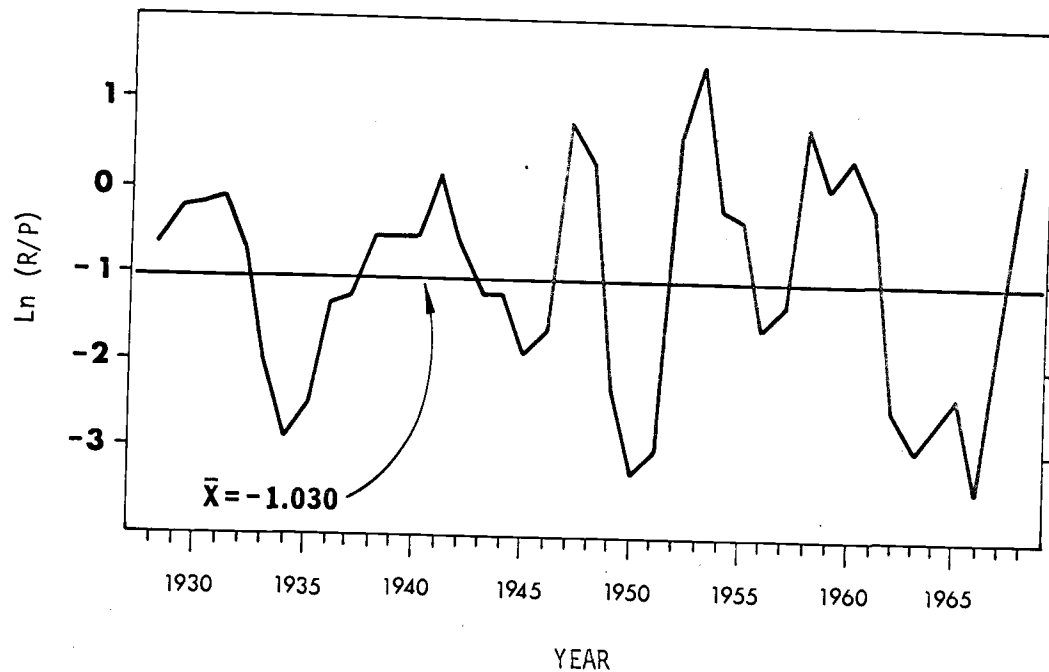


Figure 19 - Time series of the natural log of the observed recruit biomass per spawning biomass.

The similarity of the yield isopleths in four simulations with the nonlinear Ricker sea level function and varying quota levels suggests that long-term yield is not very sensitive to alterations in the quota levels (Figure 20). Mean yield also appears to be independent of age at recruitment at upper quota proportions below 0.3. At upper quota proportions above about 0.4 mean yield is influenced by age at recruitment and maximum mean yield occurs at high upper quota proportions and an age at recruitment of about 3 years old.

The 1946-1968 series of simulations made with the nonlinear Ricker transport recruitment function and the same quota levels as the previous series do not show that yield is greatly influenced by age at recruitment (Figure 21). When the quota levels are set at zero, mean yield is almost entirely dependent on the quota proportion. The exception to this is that when the quota proportions are above 0.3 the mean yield is less when age at recruitment exceeds age 3. When the upper quota level is set at 80 million pounds (36,000 metric tons) the simulations suggest that mean yield is low, around 10 to 15 million pounds (4,500 to 6,800 metric tons) over the entire range of age at recruitment and the entire range of quota proportions.

The preceeding simulations with the two environmental-dependent recruitment functions show considerable difference in mean yields. There are several reasons for this. First the recruitment functions were fitted to different time periods; the sea level function was fitted to data from 1931-1968 and the transport function included

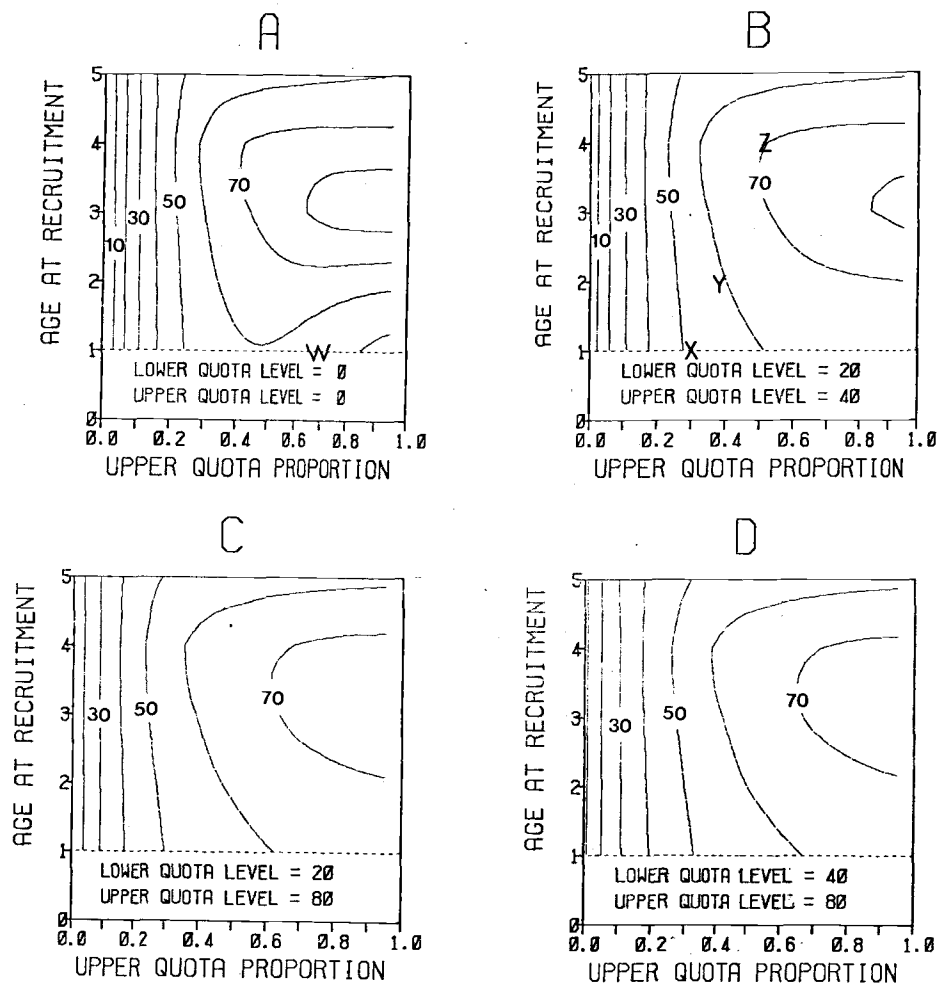


Figure 20 QUOTAE mean yield isopleths (1931-1968), at different sets of quota levels, with the Ricker sea level model. (Yield in millions of lbs, quota based on spawning biomass)

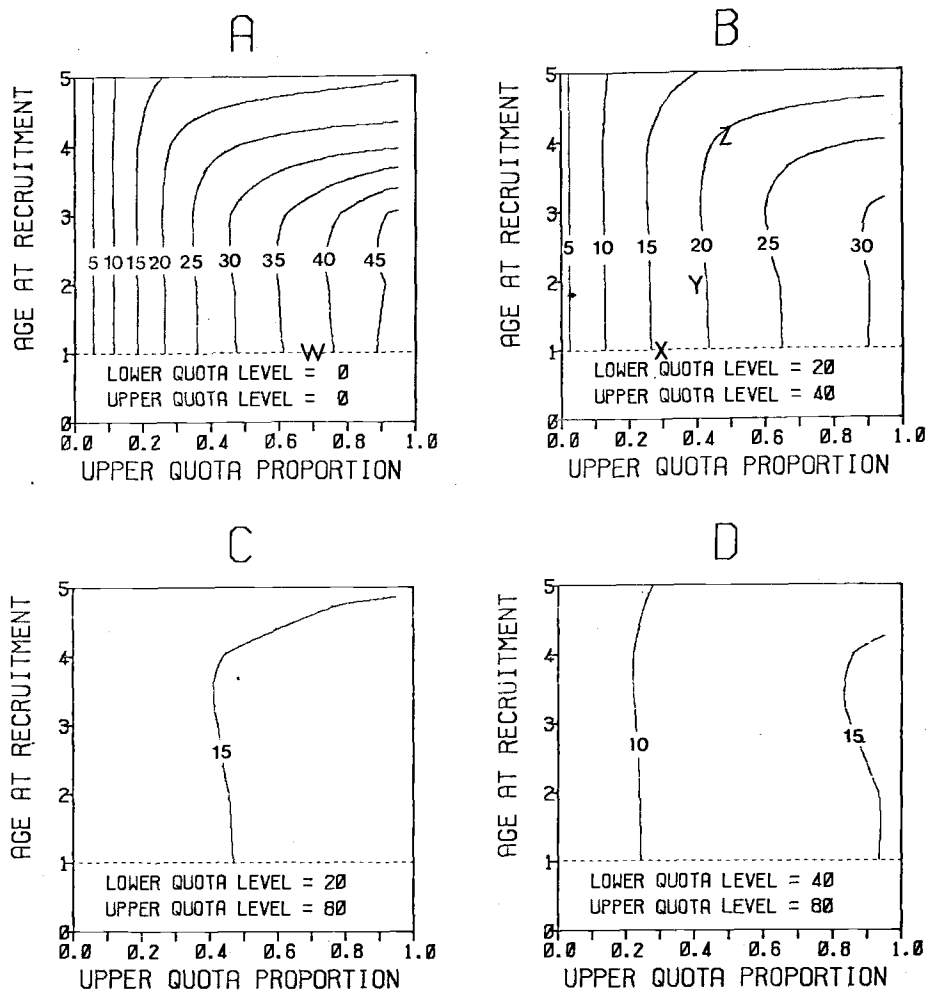


Figure 21 QUOTAE mean yield isopleths (1946-1968), at four different sets of quota levels, with the Ricker transport model (Yield in millions of lbs, quota based on spawning biomass)

data from 1946-1968. The transport function was fitted to data with a much lower mean spawning biomass and in addition about half of the years from 1946-1968 were during the periods of the sharp population declines that occurred during the early 1950's and the mid 1960's. The simulations also differ in that the starting biomass for those with the sea level function was the 1931 biomass while the transport simulations started with the 1946 biomass. The 1931 biomass was about 4.7 times larger than the 1946 biomass (611 vs 131 million pounds, 277,000 vs 59,000 metric tons). This factor of course resulted in higher mean yields in the simulations with the 1931 biomass as the starting biomass.

Annual yield under four management options

To assess the similarity of yields under the different environment-dependent recruitment functions, simulations under four management options were run. These simulations had the same time periods (1946-1968) and were initialized with the observed 1946 biomass. A third environmental-dependent recruitment function was included in this series of simulations. This recruitment function, the reduced sea level model, was included to determine if the population decline of the late 1960's would have been predicted by a recruitment function that was fitted to a reduced data set that did not include the period of the population decline.

The major difference between the yield estimates with the density-dependent and environmental-dependent recruitment functions

is the large variation in annual yield that occurs in the simulations run with the environmental-dependent recruitment functions. Time series of yields in simulations with the density functions show a stable approach to equilibrium yield. Simulations (1946-1968) with the Ricker sea level functions and the Ricker transport function show considerable variation in annual yield under different management options. Figures 22 and 23 show simulations with the Ricker sea level, reduced Ricker sea level and Ricker transport recruit functions. Simulations for each recruitment function are shown with four different management options. The first option (Figure 22A) is approximately the fishing rates that occurred in the late 1960's. The other three options are based on the California regulations and have lower and upper quota levels of 20 and 40 million pounds (Figures 22B, 23).

The Ricker sea level and reduced Ricker sea level models show essentially the same yields within each option. Yields with the reduced Ricker sea level model are always slightly higher than those with the Ricker sea level model. The reduced model was fitted to data (1931-1960) with a slightly higher mean recruitment than the Ricker sea level model (1931-1968). The Ricker transport model shows considerably higher yields than the sea level models in the simulations with an age at recruitment of 1 and a quota proportion of 0.7. Yields with the Ricker transport model under the three quota level options are considerably lower than yields with the sea level models and also much lower than yields with the Ricker transport model in the option with a quota proportion of 0.7. The reason for the much

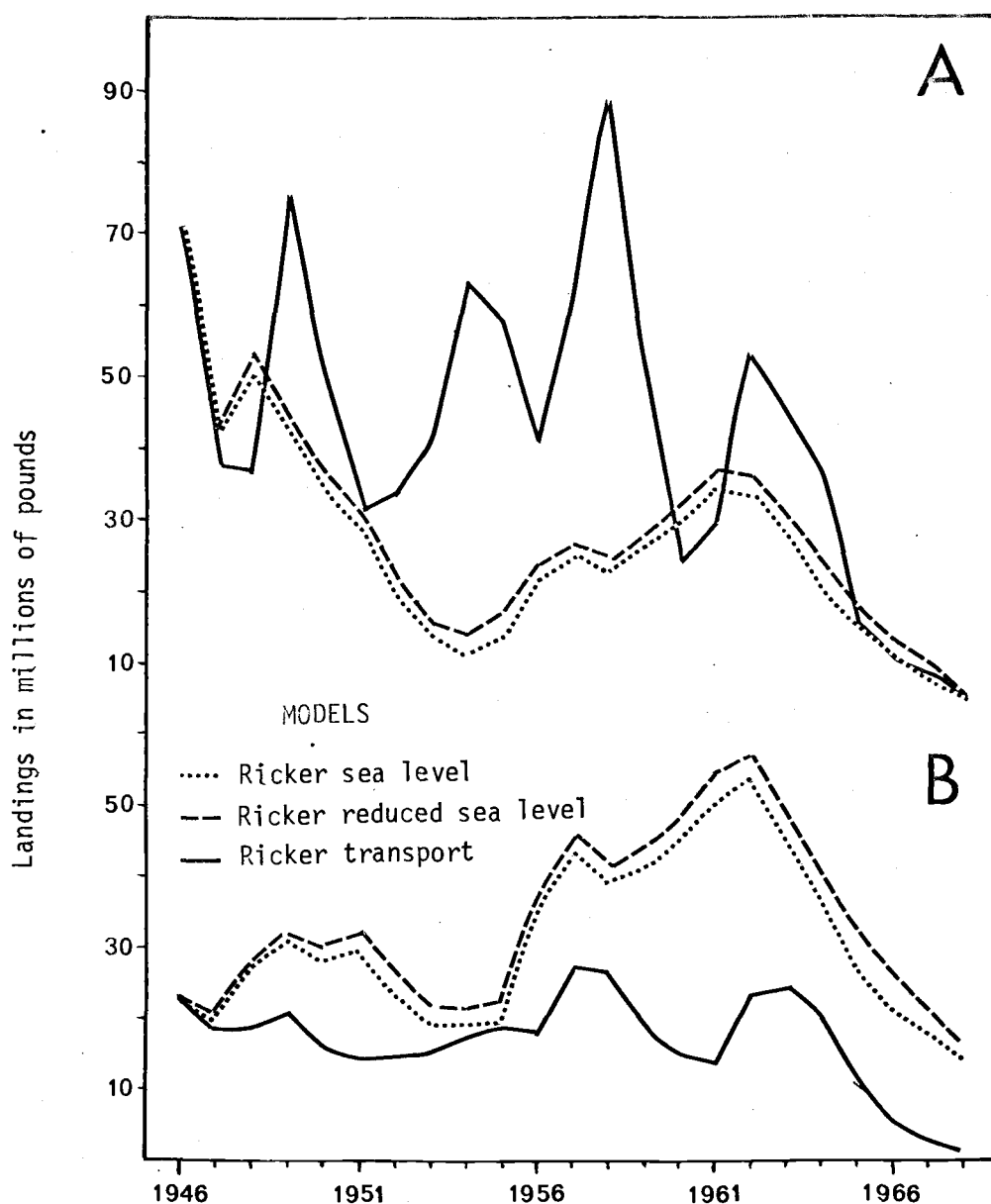


Figure 22 QUOTAE simulations (1946-1968); A. Recruitment at age 1, no minimum quota level and a quota proportion of 0.7 (w in figs 21A and 22A) B. Present California Regulations recruitment at age 1 and an upper quota proportion of 0.3 (x in figs 21B and 22B)

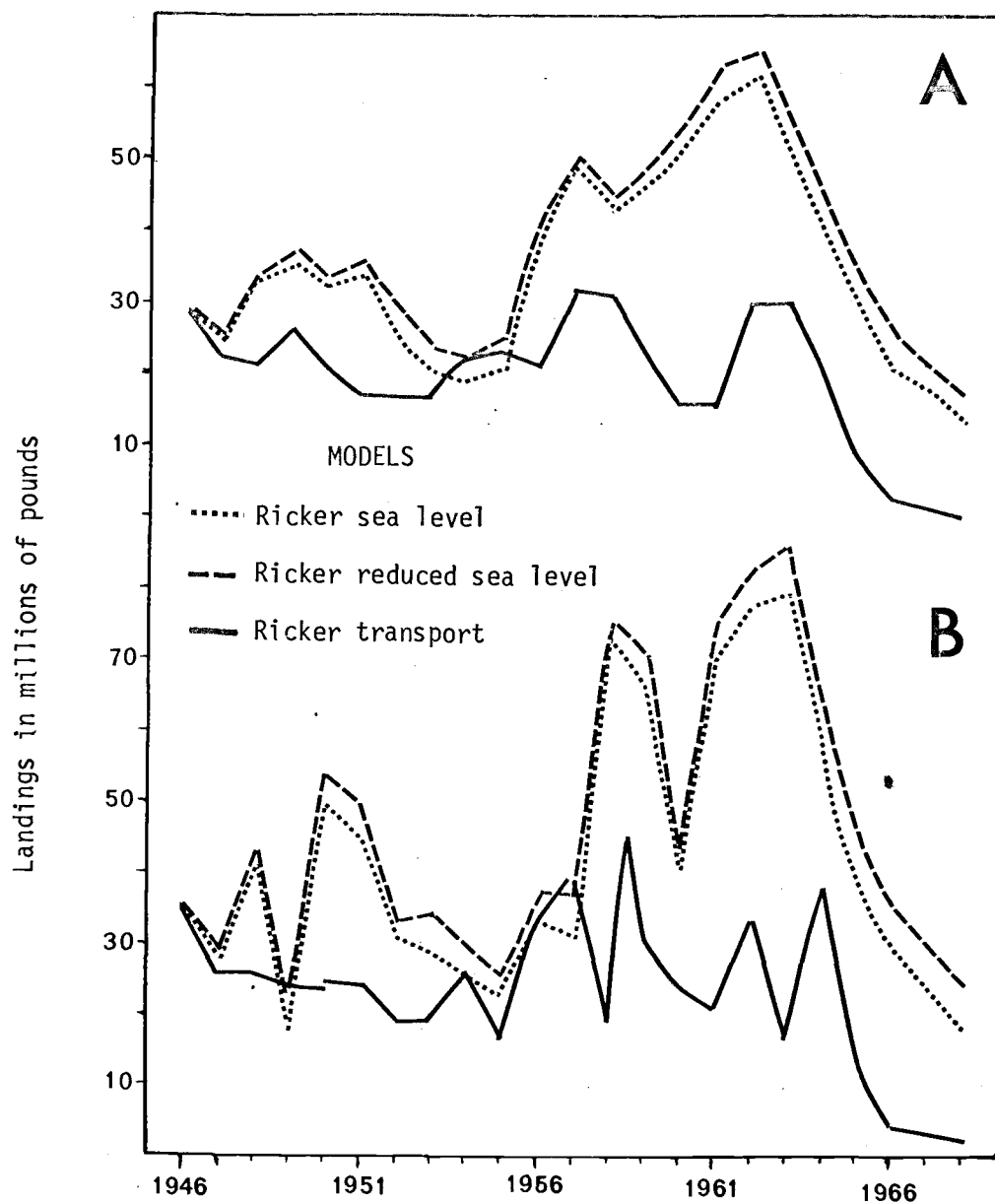


Figure 23 QUOTAE simulations (1946-1968); A. Recruitment at age 2 and an upper quota proportion of 0.4 (y in figs 21B and 22B) B. Recruitment at age 4 and an upper quota proportion of 0.5 (z in figs 21B and 22B)

higher predicted yields in the transport model with the 0.7 quota proportion is an apparent bias in the compensatory term in the Ricker function. This bias will be discussed later.

The simulations with the sea level models show considerably different yield patterns under the four management policies. For example the yields in the simulations with an exploitation rate of 0.7 show a sharp decline from 1946 to 1954 (Figure 22A). Yields declined from about 70 million pounds to about 13 million pounds and then rose to about 35 million pounds in 1961 (32,000 to 5,900 to 16,000 metric tons). By comparison, the simulation with the present California regulations, which result in an exploitation rate below 0.3, show yields of between 20-30 million pounds (9,000-13,000 metric tons) from 1946-1954 and a large increase in yields during the 1956-1966 period (Figure 23B). The heavy exploitation and resultant decrease in spawning biomass with the 0.7 quota proportion option decreased the large 1956-1966 increase in yields that is predicted by the simulations with the present California regulations. The simulations with age at recruitment of 4 (Figure 23B) show sharper variations in annual yield than with the other three options. This management option, which protects the spawning biomass, puts a very heavy exploitation rate on the 4 year olds. With this option almost the entire yield is 4 year olds and the annual yield is therefore erratic because it is dependent upon individual year classes.

The precipitous decline in the Pacific mackerel population in the late 1960's is evident in all of the simulations with environmental-dependent recruitment functions. The decline went to lower

spawning biomass levels in simulations with high exploitation rates; however, low spawning biomass also occurred in the late 1960's in simulations with no fishing mortality.

EVALUATION OF RECRUITMENT MODELS

The poor statistical fits of the density-dependent recruitment functions presented earlier (Table 3) suggests that these models are of limited use for management purposes. They could be used for long-term management purposes (i.e., to estimate long-term yields under a given exploitation rate) but should not be used for real time management. The recruitment models that include both density-dependent and environmental-dependent components (Table 4) are considerably better than the density-dependent recruitment functions in predicting recruitment in a given year. Two important questions remain. How good are the environmental models? Are the variables in the models good indices of the real mechanisms that control recruitment.

The transport models have the best statistical fits; however, they are deficient in the sense that they were fitted to a shorter data series than the sea level models. This shorter series (1946-1968) did not include any years in which the spawning biomass was at the high levels that occurred prior to the peak of the fishery in 1936. Mean recruitment during the 1946-1968 period was considerably smaller than during the 1931-1968 period. The transport models were therefore fitted to a data series that is biased towards low

recruitment. The computer simulations presented earlier show that the Ricker transport model predicts considerably smaller recruitment and yields than the Ricker sea level models and the density-dependent Ricker and Cushing models. The low estimates are not caused by the environmental terms. The low recruitment estimates with the Ricker transport model are caused by the compensatory term of the Ricker model. The 1946-1968 and 1928-1968 linear fits to the Ricker spawner-recruit model have very great differences in their density-dependent and compensatory terms.

$$1946-1968 \quad R = 1.123Pe^{-0.0000169 P}$$

$$1928-1968 \quad R = 0.508Pe^{-0.00000214 P}$$

The 1946-1968 model has a much steeper ascending curve and the compensatory term is important at much smaller spawning biomass levels. The 1946-1968 model predicts greater recruitment at low spawning biomass levels than does the 1928-1968 model. Thus the simulations with the Ricker transport model have greater yields than the Ricker sea level models when the exploitation rate is very high (Figure 22A) and smaller yields when the exploitation rate is moderate (Figures 22B, 23). The compensatory term (e^{-bP} , Table 1) for several spawning biomass levels is shown below for the nonlinear Ricker, Ricker sea level and Ricker transport models.

Model	Ricker	Ricker sea level	Ricker transport
Compensatory Term (CT)	$e^{-0.00000253 P}$	$e^{-0.00000353 P}$	$e^{-0.0000377 P}$
Spawning Biomass in millions of Pounds			
20	CT = 0.951	CT = 0.932	CT = 0.470
50	CT = 0.881	CT = 0.838	CT = 0.152
100	CT = 0.776	CT = 0.703	CT = 0.023
200	CT = 0.603	CT = 0.494	CT = 0.0005
400	CT = 0.363	CT = 0.244	CT = 0.0000003
600	CT = 0.219	CT = 0.121	CT = 0.00000000015

The above data demonstrate a major difficulty in developing regression models to describe the spawner-recruit relationship in exploited populations. Such regression models are generally lacking in data at the high spawning biomass levels that typically occur before exploitation begins. The compensatory term of the Ricker transport model is a good example of the unrealistic, yet statistically valid, regression models that can result from regressions based on data sets which do not include a good representation of data from the entire range of population biomass.

Further work that would incorporate upwelling and offshore divergence indices back to 1928 is envisioned. Barometric pressure fields are available back into early 1900's. The use of these pressure fields to calculate upwelling and offshore divergence indices will soon be in progress and further refinement of the transport models is dependent on this longer data series.

I feel that the environmental variables in the transport model (Bakun's upwelling and wind stress curl indices) are more direct estimates of the mechanisms that regulate recruitment than are the variables in the sea level models. Upwelling is obviously related to recruitment, because it determines the basic productivity of the California Current Region. Bakun and Nelson (In Press) have suggested that strong, negative wind stress curl (convergence) at 30°N would contribute to the separation of the surface waters north and south of the Punta Eugenia area. Weak, negative wind stress curl would be associated with an increase in the mixing between the two areas. Their hypothesis has several interesting features. It describes a physical boundary that explains the presence of the separate stocks of Pacific mackerel, sardine and anchovy that are found north and south of Central Baja. It also suggests that larvae from a wider geographical area could contribute to the California stock during periods of weak convergence at Punta Eugenia. A second hypothesis is that strong convergence at 30°N in the center of abundance of Pacific mackerel could be inhibitory to survival of Pacific mackerel larvae. Either downwelling or the formation of fronts could conceivably result in increased larval mortality.

The sea level models do not have as good statistical fits as do the transport models; however, they are fitted to data that includes the entire range of observed spawning biomass. The environmental variables in the sea level model (sea level, barometric pressure and sea surface temperature) are correlated with the real

environmental variables that control recruitment, but with the exception of sea surface temperature they are not direct estimates of the real variables.

Sea level at La Jolla during the spawning season is negatively correlated with recruitment. Hicks and Crosby (1974) have shown long-term increases in sea level at La Jolla and San Diego. The trend in increasing sea level could be caused by land subsidence in the La Jolla-San Diego area or a wide range of oceanographic and atmospheric factors. It is possible that the negative correlation is affected by the opposing trends of increasing sea level and decreasing population of Pacific mackerel that occur over the 1928-1968 period. This trend would not, of course, account for the seasonal pattern of correlation coefficients.

The decadal differences in sea level, between 1948-1957 and 1958-1969, at San Diego were analyzed by Huang (1972). He suggested that geostrophic flow provided the major contribution to the differences in sea level. High correlations between geostrophic flow and sea level were also found during the Coastal Upwelling Experiment (CUE); increased southward flow was associated with decreased sea level (Smith, 1974). It therefore appears that the correlation between $\ln(R)$ and sea level is a measure of the underlying relationship between recruitment in Pacific mackerel and geostrophic transport. Increased geostrophic flow in the California Current would be expected to increase the southerly advection of nutrient- and plankton-rich water from the major upwelling regions off of central

and northern California. Therefore the survival and growth of larvae in the Southern California Bight and Baja region should be enhanced by increased geostrophic flow.

Barometric pressure is a measure of atmospheric circulation, and low barometric pressure at San Diego is associated with increased winds in the southern end of the California Current. Barometric pressure is therefore an index of upwelling in this region.

The positive correlation between sea surface temperature and recruitment is expected. Warm SST should favor recruitment in the California Current stock of Pacific mackerel, because this stock is on the cold-water edge of its potential range. However, this correlation would seem to be in contradiction with the correlation between upwelling and recruitment. If increased upwelling occurs during the spawning season SST should be reduced. It is possible that SST is influenced by the spacing of upwelling events, being lower if upwelling is more continuous and higher if upwelling events are followed by periods of calm weather with considerable insolation (a condition that should favor recruitment). Upwelling prior to the spawning season would also tend to decrease SST and possibly increase the number of planktonic predators. Large scale SST anomalies unrelated to upwelling in the northern Baja area could also increase SST in this area.

Simulations with the density-dependent recruitment functions predict that at high exploitation rates equilibrium yield is quite sensitive to changes in the age at recruitment. Maximum yield with

the nonlinear Ricker and Cushing spawner-recruit functions occurs at exploitation rates above 0.3 and at an age of recruitment of between 3 and 4 years of age. If the fishery were to be managed with the present California regulations, the Ricker function predicts that equilibrium yield would be about 67 million pounds (30,000 metric tons) per year (X in Figure 18B). The simulations suggest that equilibrium yield could be increased to over 95 million pounds (43,000 metric tons) if the upper quota proportion were increased to 0.5 and the age at recruitment increased to age IV (Z in Figure 18B). This large an increase in potential yield is not predicted by comparable simulations with the environmental-dependent recruitment functions. Simulations with the sea level spawner-recruit function predict that mean yield for the period of 1931-1968 would have been just over 51 million pounds (23,000 metric tons) if the present California regulations had been in effect over this period (X in Figure 20B). Observed yield for this period averaged 49 million pounds (22,000 metric tons). The above simulation predicts that mean yield would have increased to 69 million pounds (31,000 metric tons) if the quota proportion had been set at 0.5 and the age at recruitment had been IV (Z in Figure 20B). The highest age at recruitment that could practically be considered for the Pacific mackerel fishery is age 2. This is due to the mixed schooling of different age groups of mature Pacific mackerel. When the age at recruitment is set at age 2 the equilibrium yield with the Ricker model is a maximum of

75 million pounds (34,000 metric tons) at an upper quota proportion 0.4 (Y in Figure 18B). The Ricker sea level model predicts that the mean yield under this management (Y in Figure 20B) would have been 60 million pounds (27,000 metric tons).

The Ricker sea level model predicts that the mean annual yield over the period of 1946-1968 would have been 31 million pounds (14,000 metric tons) if the California regulations had been enacted in 1946. The observed mean yield over this period was 31 million pounds. Mean yield over this period with an age at recruitment of 2 and an upper quota proportion of 0.4 is predicted at 35 million pounds (16,000 metric tons). The corresponding predictions with the Ricker transport model (Figure 22) are 16 and 19 million pounds (7,200 and 8,600 metric tons).

It appears that the simulations with the Ricker sea level model are more realistic than those with the Ricker transport model. Yields with the environmental models are considerably lower than those predicted by the equilibrium simulations with the density-dependent recruitment models. The yield per recruit simulations (ISOE) predict that maximum yields on an individual cohort occur at an age at recruitment of less than 1 and at high fishing mortality rates. Spawning biomass levels with this management policy are minimal and long term yield under this policy is low in both the equilibrium and environmental-dependent simulations with the QUOTAE program.

The predictive capability of recruitment in a given season is highest with the transport models. The Ricker transport model

accounts for over 75% of the variation in recruitment for the period of 1946-1968. It would be desirable to test the predictive capabilities of the various recruitment models with data from years outside of the period for which the models were fitted. Unfortunately good quality population estimates are not available for the period of 1970-1975. This lack of data was caused by the moratorium on the commercial fishery. The moratorium halted the market sampling program from which age composition data was derived. Estimates of the population size and recruitment for the 1970-1975 period therefore cannot be based on a cohort analysis. Available estimates on the recent spawning biomass are based on small scale tagging studies, and estimates of recruitment during the 1970-1975 period are not available. However, the environmental portion of the Ricker transport model predicts that from 1963 to 1975 there were no years in which the environmental conditions greatly favored recruitment. Moderately good environmental conditions were predicted in 1971, 1972 and 1974.

FACTORS AFFECTING RECRUITMENT

The spawning biomass of Pacific mackerel undoubtedly establishes the limits on the possible size of an individual year class. Within these limits recruitment is heavily dependent upon physical environmental conditions. Interrelations with other species also play a role in determining recruitment (Hunter 1976). However, the direct relationship between the populations of other species and recruitment

in Pacific mackerel is difficult to demonstrate with available data.

Over the period of 1928 to 1968 the estimated recruit biomass varied from 0.58 to 321 million pounds (260 to 145,603 metric tons). Recruitment success therefore varied by a factor of 560. Density-dependent recruitment models account for a maximum of about 24 percent of the variation in recruitment. Recruitment models incorporating both density-dependent terms and environmental terms account for about 60 percent of the variation in recruitment from 1931-1968 and about 75 percent of the variation from 1946 to 1968. Year-classes in excess of 100 million pounds (45,000 metric tons) at age 1, occurred in only 9 of the 41 years. In only one of these 9 years was the spawning biomass below 100 million pounds (57 million pounds). The spawning biomass exceeded 100 million pounds in 24 of the 41 years. This suggests that strong year-classes are most likely to be produced in years with both good environmental conditions and a large spawning biomass. It also suggests that given a reasonably large spawning biomass the principal limiting factor in recruitment is not a density-dependent factor. When either a heavy fishery or a series of years with unfavorable environmental conditions occurs (and particularly when both occur together) the future spawning biomass is likely to fall to levels where even optimum environmental conditions cannot produce a strong year-class. In these situations the spawning biomass becomes the limiting factor.

In the California Current stock the critical spawning biomass of Pacific mackerel appears to be around 20 to 30 million pounds. With this level of spawning biomass a strong year-class could occur only with the very best environmental conditions. At spawning biomass levels above this critical level recruitment will be progressively less influenced by the spawning biomass level. However, the pattern of variation of the annual environmental conditions appears to be the factor which has the greatest control over the Pacific mackerel population.

There has been much discussion of the role of the "critical period" in the determination of year class strength. The term "critical period" has been used to cover what I feel are two distinct processes in larval survival of pelagic fishes. The first is the "critical period" in the usage of Hjort (1926), the period just after the yolk sac is absorbed. It is best characterized as time of first feeding. Density-dependence, within the cohort, is not likely to be of great importance to survival through first feeding or until the larvae are several weeks old and greatly increase their mobility. The total number and concentration of eggs in a single spawning spot will affect early survival within the individual spawning spot. During the early larval period mortality of larvae will primarily be dependent upon the following factors.

1. The amount and type of plankton in the immediate proximity of the spawning spot.
2. The concentration of planktonic predators in the vicinity of the spawning spot.

3. Predation by nekton.

The first two factors have undoubtedly contributed to selection for an optimum size and density of individual spawning spot. The larvae in this optimum spawning spot must be dense enough to satiate background predation by planktonic predators and at the same time sparse enough to insure that the density of planktonic food is sufficient to allow feeding and growth through the early, relatively non-mobile larval stages. Density-dependence in the survival of a cohort through this early feeding stage is likely to be a function of the combined biomass of the entire trophic level. If the biomass of small pelagic fishes is large in relation to the amount of plankton present prior to spawning the plankton concentration is likely to be too low to allow good larval survival and therefore a poor year-class will result. Cushing (1974) has suggested that density dependence within their trophic level is a major factor in the sardine-anchovy relationship in the California Current.

The above considerations have, in my opinion, selected for a reproductive pattern for Pacific mackerel (and other pelagic fishes in upwelling regions) in which the size of spawning schools is much smaller than the size of schools during the rest of the year. Little is known of the spawning behavior and spawning school size in mackerel; however, ripe fish are extremely rare in the commercial landings and purse seiner catches have traditionally been very small

during the peak of the spawning period. Thus, it appears likely that optimum spawning school size is relatively small, at least too small to justify a purse seine set.

Lasker (1975) has suggested that virtually all of the survival of first-feeding anchovy larvae is linked to relatively rare patches of suitable-sized phytoplankters. He also observed that chlorophyll maximum layers that contain phytoplankters of suitable size for first-feeding anchovy larvae are likely to be completely dispersed by a single storm. This observation implies that survival through the first feeding could be heavily influenced by the periodicity of individual upwelling events. Closely spaced storms, while providing sufficient nutrients for rapid phytoplankton growth, may prevent the development of the dense concentrations of phytoplankters required for first-feeding larvae. Storms followed by a week to 2 weeks of relatively calm weather may therefore be a requirement for good survival through first feeding. If the interval between upwelling events is too great, total production will be lowered and the survival of older larvae will be reduced.

The second mechanism affecting larval survival occurs during the late-larval and post-larval stages, when the fish are mobile enough to allow mixing between the survivors from different, more widely separated spawning spots. Mackerel in these developmental stages would be able to swim only relatively short distances and their distribution would still be heavily dependent on prevailing

surface currents. During this period density-dependent mortality could be grouped into the following categories:

1. Mortality dependent upon density within the cohort. Such mortality may be of two types.
 - a. Mortality resulting from competition for the same food source. This type of mortality could conceivably result in a recruitment function similar to the Ricker model where a very large biomass can result in poor recruitment.
 - b. Intraspecific predation of eggs and larvae spawned late in the spawning season by the survivors from earlier spawning. This type of mortality would reduce the number of recruits-per-spawner but is not likely to reduce total recruitment. Mortality of this type is likely to result in a recruitment function of the type used by Cushing (1971).
2. Mortality dependent upon density within the species (i.e., older cohorts).
3. Mortality dependent upon the biomass of the entire trophic level.

Because of their relatively large mouth, late-larval and post-larval mackerel probably feed on larger particle size food than the anchovy or sardine larvae. However, a comparison between the food of these mackerel and pre-adult or adult mackerel is probably impossible with present knowledge. Pre-adult and adult anchovies

and sardines undoubtedly feed on the same food organisms as post-larval mackerel. The amount and density of food available to late and post-larval mackerel is dependent on relationships between the production of plankton and the grazing of plankton by organisms at the same or lower trophic levels as the mackerel. It is difficult therefore to separate items 2 and 3 above.

Environmental-dependent mortality will be principally dependent upon primary production prior to and during the larval stages and upon surface transport of the fish during their relatively non-motile stages. Thus upwelling, divergence-convergence patterns, and geostrophic flow will heavily influence the proportion of prejuvenile fish that will contribute to the recruitment of Pacific mackerel in the California Current Region.

The use of the term environmental-dependent mortality does not necessarily imply that this mortality is either density independent or density dependent. For example mortality of larvae may be greater during a spawning season with reduced upwelling and the mechanism of this mortality may be density related. Conversely, transport of larvae out of the California Current area could be entirely density-independent. It should be emphasized that recruitment is an interplay between environmental factors and spawning stock size and therefore density-independent fluctuations and density-dependent relationships are not separate halves of the process.

The large environmentally related fluctuations in recruitment of Pacific mackerel suggest that the recovery of the stock is more likely to be related to environmental conditions than to the resiliency of a population that is under carrying capacity. The resiliency could be further reduced if a depensatory mortality factor becomes significant. Clark (1974) suggested that a depensatory factor could be associated with the collapses of the populations of pelagic schooling fishes. The mechanism suggested by Clark, increased mortality due to a reduction of the size of schools, is not likely to result in critical depensation because the Pacific mackerel sub-adults and adults commonly school with jack mackerel. A second mechanism, increased larval mortality due to suboptimum spawning school size, could result in critical depensation and long-term loss of the stock.

RECOMMENDATIONS

There is considerable variation in the Pacific mackerel management policies that would be developed with the several modeling approaches contained in this study. Policies based on yield per recruit simulations would favor the very high exploitation rates and an age at recruitment of 1 or less that are necessary to achieve maximum yield per recruit. Equilibrium yield simulations based on the Cushing or Ricker spawner-recruit models suggest that near maximum sustained yield (MSY) would be achieved with a wide range of exploitation rates ($E = 0.3$ to 0.6) and an age at recruitment of age 3 or 4. With a management policy based on a maximum yield per recruit philosophy equilibrium yield simulations based on the Ricker spawner-recruit model predict that the stock would become extinct. Similar simulations with the Cushing spawner-recruit model predict that yields would be well below MSY.

Simulations with a wide range of quota options and the environmental-dependent recruitment models suggest that no management policy is likely to stabilize the yield at reasonably high levels. The best management policy therefore appears to be one that will reduce the possibility of future population collapses and at the same time achieve a maximum longterm yield. That is a policy that will reduce the exploitation rate when the population level is low and increase the exploitation rate when the level is high.

Determination of the optimum management policy will require considerable economic analysis and is therefore beyond the scope of the present work. However, in the absence of such analyses I feel that the list of potentially optimum management policies can be reduced to three alternatives. These alternatives are maximum long-term yield with an age at recruitment of 1, 2, or 3. The reason that maximum longterm yield is likely to be close to optimum yield is due to a combination of biological and economic factors. The stock is a member of a multispecies wetfish fishery and it is of secondary importance in this fishery. The stock is very available to the fishery and the fishing fleet has demonstrated that it is capable of harvesting Pacific mackerel at rates in excess of their reproductive potential. The economics of the fishery are primarily dependent upon relationships with the more abundant species in the fishery (i.e. presently anchovy). In addition the price for Pacific mackerel has traditionally been higher than the price for the more abundant species in the fishery. Economics are therefore unlikely to be the limiting factor in the Pacific mackerel fishery and maximum economic yield will approach maximum biological yield.

The three recommended management policies (Table 5) are based on the quota proportions that resulted in the maximum predicted longterm yield with an age at recruitment of 1, 2 and 3. All three management policies contain portions of the present California regulation. Specifically they maintain the present moratorium, or lower quota level, at 20 million pounds spawning biomass to ensure a viable

TABLE 5. RECOMMENDED MANAGEMENT OPTIONS*

Management Option 1 The present California regulations.

No minimum size restrictions
 Quota levels of 20 and 40 million pounds
 Lower quota proportion of 0.2
 Upper quota proportion of 0.3
 Predicted long-term yield
 50 million pounds per year
 22,600 metric tons per year
 \$2,130,000 per year at \$85 per short ton

Advantages

Status Quo
 Least amount of regulation of the fishery

Disadvantages

Long-term yield is the lowest of the 3 options
 Age structure will be the most altered

Management Option 2 Compromise option

Minimum size restriction to protect 1 year olds
 Quota levels of 20 and 40 million pounds
 Lower quota proportion of 0.2
 Upper quota proportion of 0.5
 Predicted long-term yield
 64 million pounds per year
 29,000 metric tons per year
 \$2,720,000 per year at \$85 per short ton

Advantages

Long-term yield is increased without precluding a purse-seine fishery

Disadvantages

Size restriction will increase the fishing effort necessary to catch the quota

TABLE 5. RECOMMENDED MANAGEMENT OPTIONS* (cont.)

Management Option 3 Near MSY option

Minimum size restriction to protect 1 and 2 year olds

Quota levels of 20 and 40 million pounds

Lower quota proportion of 0.2

Upper quota proportion of 0.7

Predicted long-term yield

76 million pounds per year

34,500 metric tons per year

\$3,230,000 per year at \$85 per short ton

Advantages

Largest long-term yield

Least altered age structure

Disadvantages

Annual yield is the most variable

Size restrictions will preclude a purse seine fishery

Enforcement costs will be the highest

*It should be noted that the recommended management options are for the total catch, including the sport and commercial fisheries of Mexico and California.

sport fishery. They have a lower quota proportion of 0.2 and an upper quota level of 40 million pounds to allow only a minor fishery when the spawning biomass is relatively small.

CONCLUSIONS

The success in describing past recruitment in Pacific mackerel with statistical fits to environmental and population data does not prove that the factors found to be associated with recruitment are those that control recruitment. It is also possible that these environmental factors may not continue to be associated with recruitment in future years. The decision to tentatively accept the hypothesis that recruitment can be predicted with more accuracy if the associated environmental factors are taken into consideration should only be made if the environmental factors make biological sense. I believe that a very strong case can be made that the environmental factors found to be associated with recruitment are in fact those that describe major components of the mechanisms that control the mortality of pelagic fish eggs and larvae in the California Current Region.

Before arguing this case I would like to present the principal hypothesis formulated during the course of this study. This hypothesis is outlined below.

1. The survival of large numbers of pelagic eggs and larvae of the commercially important pelagic fishes of the California Current is primarily dependent upon the environmental conditions occurring in the area off central Baja California and in the Southern California Bight.

2. The major mechanisms controlling the mortality of epipelagic fish eggs and larvae in the California Current Region are upwelling and surface transport patterns.

3. It is unlikely that any commercially important species can maintain a large resident population in the region between Cape Mendocino and Point Conception if the species has epipelagic eggs and larvae.

4. The commercially important species in the California Current Region are those that have solved the early mortality problem by either migrating to the region between Point Conception and Punta Eugenia for spawning or by developing reproductive patterns that avoid epipelagic eggs and early larvae.

Much of the above hypothesis is not new. The importance of central Baja as spawning grounds for Pacific mackerel (Fry 1936b) and sardine (Ahlstrom 1954) has been known for years. It was also realized that upwelling and surface current patterns are important in the early survival of larvae in the California Current Region (California 1952). There has, however, been little documentation of the relationships between these environmental factors and survival to recruitment. Discussion of the effects of these environmental factors has been limited to the major epipelagic species. It is important to note that most of the species that do not have epipelagic eggs and early larvae do have epipelagic phases in their life history.

Before defending the above hypothesis I feel it is necessary to present some background on the various components of the currents in the California Current Region. The dominant components of the currents in this region are geostrophic transport and transport associated with wind stress. The major features of the geostrophic flow are readily seen in a figure prepared by Craig Nelson of the Pacific Environmental Group of the National Marine Fisheries Service (Figure 24). In the region from Cape Mendocino to the northern edge of Baja California the geostrophic flow is strongest at about 200 miles offshore and its direction is southerly and parallel to the coastline. Within the above region the only area with a mean northward geostrophic flow is in the area just south of Point Conception in the Southern California Bight. The northern Baja California area, south to about Punta Eugenia is unique in that the major geostrophic flow is towards the coast. With the exception of the previously mentioned area just south of Point Conception and possibly the area off of the State of Washington, the northern Baja region is the only area in the California Current where the prevailing geostrophic flow will bring planktonic eggs and larvae towards the shore. Inshore of the California Current the southern California gyre could be an important mechanism for the return of offshore eggs and larvae to the inshore area. However, this gyre is not strongly developed during the peak of upwelling in the northern Baja and southern California area. Reid and Mantyla (1976) report that off

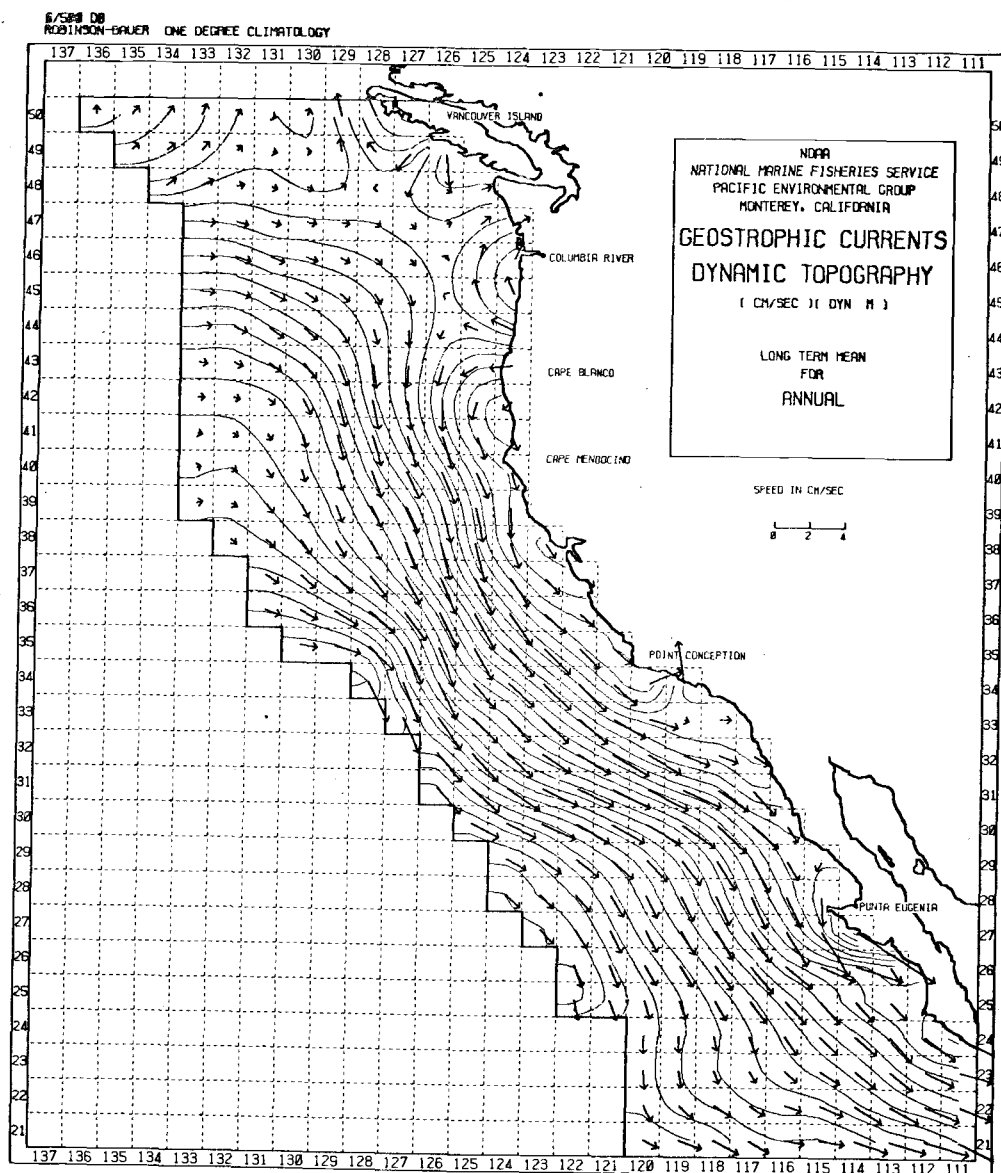


Figure 24 Geostrophic currents in the California Current Region (Nelson pers. comm.)

southern California the inshore flow is strongly southeastward in April and May and northwestward during the rest of the year, particularly in October-January.

The other major component of the current structure is that caused by wind stress. The prevailing winds in the region from Cape Mendocino to Punta Eugenia are parallel to the coast and the major component of Ekman transport is thus offshore. Bakun's (1973) upwelling indices (i.e. Ekman transport positive offshore) show that south of Cape Mendocino monthly means of Ekman transport are nearly always offshore. On a shorter time scale Bakun (1975) has shown that daily and weekly mean onshore Ekman transport is rare between San Francisco and southern Baja California and that onshore Ekman transport near Cape Mendocino is largely limited to the winter months.

The other significant feature in the surface currents is the geographical pattern of divergence of Ekman transport. The presence of a wind stress maximum well offshore implies that the surface water will be divergent out to this wind stress maximum. Upwelled nutrients, food organisms, and fish eggs and larvae in the upper layer will all tend to be swept offshore. Frontal formation and the resultant concentration of planktonic organisms will be minimal within the area of divergence. The region around 30°N , near Punta Eugenia, is also unique in that this is the only region in the California Current south of Cape Mendocino where the wind stress maximum is against the coastline. The divergence-convergence pattern in this region is shown in

Figure 10. The area just north of Punta Eugenia is the only area south of Cape Mendocino where convergence normally occurs inshore.

The above description of the dominant aspects of the current structure of the California Current Region is broken into the various components. The components are of course all operating at the same time and it is the combined effect that determines egg and larval mortality. What then is the net effect on larval transport in the areas between Cape Mendocino and Punta Eugenia? The descriptions presented above have largely described the annual means and seasonal variation has been neglected. Is it possible that at different seasons the above hypothesis and descriptions will not hold? In answer to the above questions it is pointed out that nearly all of the commercially important fishes in the California Current Region are either late winter or spring spawners. That is to say, they spawn during the beginning of the upwelling season or during the peak of the upwelling season. The annual picture of the currents is similar to that occurring during the upwelling season and the annual descriptions above essentially describe the currents during the upwelling season. Nelson's (1976) analysis of wind stress and wind stress curl over the California Current shows that there are major seasonal changes in the magnitude of the mean monthly wind stress field in the Cape Mendocino to Baja region. However there is little seasonal variability in the direction of wind stress in this region. This is not the case north of Cape Mendocino where there are strong seasonal variations in both magnitude and direction of wind stress.

The defense of the hypothesis outlined earlier can be made by considering the likely fate of a planktonic fish larva spawned inshore in various locations between Cape Mendocino and Punta Eugenia. Between Cape Mendocino and Point Conception planktonic larvae will be carried south by geostrophic transport and offshore by Ekman transport. Convergence does not occur until the larvae are several hundred miles offshore where the larvae may be of considerable help as food to the albacore population, but they are likely to be unable to return to their own populations. Planktonic larvae in the Southern California Bight are carried southeast by geostrophic transport and offshore by Ekman transport. Convergence occurs several hundred miles offshore. However, as the magnitude of geostrophic transport is greater than that of Ekman transport, the net transport of larvae carried offshore from the Southern California Bight will be towards northern Baja. Planktonic larvae in the northern Baja region will be carried towards Punta Eugenia by geostrophic transport. Ekman transport will be offshore; however, as the region of convergence extends in to the coastline at this latitude, frontal formation will reduce offshore transport. At this point I would again refer the reader to Figure 4 which shows the distribution and relative abundance of Pacific mackerel larvae.

If conditions for larval survival are so poor in the region between Cape Mendocino and Point Conception, why does this region have valuable commercial fisheries with a rapidly increasing interest to foreign fishing fleets? The answer is that the fishes of this area

have adapted their reproductive biology to reduce the loss of epipelagic eggs and larvae. Such adaptations have taken many forms. The Pacific mackerel, and particularly the sardine and hake, make long migrations to spawn in the Southern California Bight and northern Baja area. They then return northwards for feeding in the upwelling region north of Point Conception. Many species get out of the ocean entirely for spawning, i.e., salmon, steelhead, shad, and striped bass. Many species attach their eggs to the bottom in estuaries or protected bays, i.e., herring, lingcod and squid. Another successful adaptation is to spawn in deep water thus avoiding offshore Ekman transport, i.e., Dover sole, sablefish and petrale sole. Another way to reduce the loss of larvae, through larval drift, is to produce large mobile larvae. The livebears such as the rockfishes and embiotocids are good examples of fishes which have this life history strategy.

Most of the above adaptations to avoid the loss of planktonic eggs and larvae are successful in avoiding the mortality at early developmental stages. Late larval and prejuvenile stages will still be susceptible to loss by offshore transport. Coastal eddies, the narrow California Counter Current, and variations in the surface transport patterns will alter the loss of prejuvenile fishes. This alteration will affect the recruitment of the individual species and will probably cause considerable variation in the biomass of individual species. It will also contribute to variations in the total biomass of fishes in the California Current Region.

Management of the fish stocks in the California Current Region must recognize that varying environmental conditions will cause large variations in the recruitment of commercially important species of the California Current. If this factor is not recognized and incorporated in management policies, it is very likely that overfishing will occur during a period of poor recruitment and the list of populations in the California Current that have suffered recruitment failure will include species other than the Pacific sardine and the Pacific mackerel.

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APPENDIX I. YIELD PER RECRUIT SIMULATION PROGRAM.

PROGRAM ISOE (INPUT,OUTPUT,PUNCH)

```

C      YIELD PER RECRUIT MODEL          RH PARRISH  MAY 10,1976
C
C      CONTROL CARD VARIABLE DESCRIPTION
C      NRUNS      NUMBER OF RUNS TO BE MADE
C      KARD       CARD OUTPUT KARD=1 NO CARD OUTPUT KARD=C
C      TITLE      TITLE LIMITED TO 80 CARD COLUMNS
C      IBERT      IBERT=1 IF BERTALANFFY GROWTH EQUATION IS USED
C      MAXA       MAXIMUM AGE OF THE SPECIES
C      IBT        MINIMUM AGE AT RECRUITMENT
C      IET        MAXIMUM AGE AT RECRUITMENT
C      XMS        STARTING INST. NATURAL MORTALITY RATE (M)
C      XMI        M INCREMENT
C      NM         NUMBER OF M S TO BE RUN
C      EINC       EXPLOITATION RATE INCREMENT
C      NE         NUMBER OF EXPLOITATION RATES TO BE RUN
C      LINF       BERTALANFFY CONSTANT
C      K          BERTALANFFY CONSTANT
C      TO         BERTALANFFY CONSTANT
C      A          LENGTH-WEIGHT CONSTANT
C      B          LENGTH-WEIGHT CONSTANT
C      PS(1)      PROPORTION SPAWNING BY AGE GROUP
C                  ONLY INPUT FOR AGES IBT TO 10 (10+ ARE ASSUMED 1.0)
C
COMMON M,IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50)
1,KARD
DIMENSION BC(20,50),PS(51),G(51),GH(51),WT(51),XH(51),XL(51),
1XLW(51),TC(20),TITLE(20)
INTEGER T
REAL M,LINF,K
READ 399, NRUNS,KARD
399 FORMAT (2I2)
1 NRUNS=NRUNS-1
READ 400,(TITLE(I),I=1,20)
400 FORMAT(10A8,/,10A8)
PRINT 401,(TITLE(I),I=1,20)
401 FORMAT(1H1,/,1X,10A8,/,1X,10A8)
READ 100,IBERT,MAXA,IBT,IET,XMS,XMI,NM,EINC,NE
100 FORMAT (4I3,2F5.3,I3,F5.3,I3)
IF (IBERT.NE.1) GO TO 2
READ 101 , LINF,K,TO,A,B
101 FORMAT(F10.2,F10.6,F15.9,F15.12,F10.6)
PRINT 102, LINF,K,TO,A,B
102 FORMAT (15,'BERTALANFFY CONSTANTS',/,T8,'L INFINITY =',F10.2,/,
178,'K =',F10.6,/,I3,'TO =',F10.6,/,I5,'LENGTH-WEIGHT CONSTANTS
2',/,T8,'A =',F15.12,/,T8,'B =',F10.6,/)
GO TO 4
C      ADD OTHER INPUT OPTION
2 CONTINUE
READ 666,(WT(N),N=1,10)
666 FORMAT (10F6.2)
READ 668,(PS(N),N=1,10)
668 FORMAT (10F6.4)
DO 670 N=11,51
670 PS(N)=1.0
DO 671 N=1,14
TEMP=WT(N+1) / WT(N)
671 G(N)=GH(N)=TEMP
DO 672 N=15,MAXA
GH(N)=G(N)=TEMP
672 WT(N)=WT(N-1)* TEMP
IF (IBERT.EQ.0) GO TO 7

```

```

      GO TO 38
4   DO 5 I=1,51
5   PS(I)=1.0
      READ 103,(PS(I),I=1B7,10)
103  FORMAT(10F6.4)
      IA=MAXA+1
      DO 6 N=1B7,IA
      XL(N) = LINF* (1-EXP(-K*N + K*TO))
      U = N + 0.5
      XLH(N) = LINF* (1-EXP(-K*U + K*TO))
      WT(N) = A*XL(N)**B
      WH(N) = A*XLH(N)**B
      GR(N) = WH(N)/WT(N)
      IF (N.GT.1B7) G(N-1) = WT(N)/WT(N-1)
6   CONTINUE
C   NOTE THAT THE UNITS ARE DEPENDENT UPON INPUT
7   PRINT 200
200  FORMAT (//,1X,*AGE   LENGTH   WEIGHT           PS      GRCH   GROWH*)
      DO 8 N=1B7,MAXA
      PRINT 104,N,XL(N),WT(N),PS(N),G(N),GR(N)
104  FORMAT (1X,13,2F9.2,3F9.3)
8   CONTINUE
      M=XMS-XMI
      DO 26 NM=1,NM
      TOT(NM)=0
      M=M+XMI
      E=-EINC
      DO 24 J=1,NE
      E=E + EINC
      F=E 3      N=0
      IF(E.EQ.0) GO TO 12
10  N=N+1 5      IF(N.GT.50) GO TO 90
      EV=EVAL(F)
      E1=EVAL(F-0.01) 5 E2=EVAL(F+0.01)
      SLOPE=(E2-E1)/0.02
      DIFFE=EV-E
      F=F-DIFFE/SLOPE
      IF(ABS(DIFFE).GT.0.000001) GO TO 10
12  FST(J)=F
      Z=M+F
      DO 22 I=1B7,JET
      HS = C = 0
      POP=1000
      DO 20 T=1B7,MAXA
      IF(I.GT.1B7) GO TO 15
      IF(F.EQ.0) TOT(NM)=TOT(NM)+POP
      IF(F.EQ.0) BC(NM,T)=POP
15  HS=HS + POP*PS(T)
      IF (T.LT.I) GO TO 14
      W=Z
      FF=F
      GO TO 16
14  W=M
      FF=0
16  D=POP*(1-EXP(-h))
      IF(FF.EQ.0) GO TO 18
      C=D*(FF/Z)*GH(T) + C
18  POP=(POP-D) * G(T)
20  CONTINUE
      IS(I,J) = HS
      IY(I,J) = C
22  CONTINUE
24  CONTINUE
      PRINT 105,M

```

```

105 FORMAT (//,31X,*YIELD PER METRIC TON OF RECRUITS M=*,F6.4,/,
1* AGE*,36X,*(IN KG.)*,/,* AT*,/,* REC.*)
CALL OUTISO(IY)
PRINT 110,M
110 FORMAT (//,31X,*SPAWNING BICMASS OVER LIFE OF COHORT F=*,F6.4,
1//,* AGE*,/,* AT*,/,* REC.*)
CALL OUTISO(IS)
26 CONTINUE

PRINT 111
111 FORMAT (//,31X,*BICMASS CURVES WITH NO FISHING MORTALITY*//,1X,
1*AGE INSTANTANEOUS NATURAL MORTALITY*//)
M=XMS-XMI
DO 28 N=1,NM
M=M+XMI
28 FT(N)=M
PRINT 112,(FT(N),N=1,NM)
112 FORMAT (7X,20F6.2)
IYR=IBT-1
DO 30 I=IBT,MAXA
IYR=IYR+1
PRINT 113,IYR,(BC(MM,I),MM=1,NM)
113 FORMAT (1X,I4,2X,20F6.0)
30 CONTINUE
DO 34 MM=1,NM
DO 32 I=IBT,MAXA
BC(MM,I)=EC(MM,I)/TC7(MM)
32 CONTINUE
34 CONTINUE
PRINT 115
115 FORMAT (//,31X,*PROPORTION OF THE POPULATION BY WEIGHT F=0*,
1//,* AGE INSTANTANEOUS NATURAL MORTALITY*//)
PRINT 112,(FT(N),N=1,NM)
IYR=IBT-1
DO 36 I=IBT,MAXA
IYR=IYR+1
PRINT 116,IYR,(BC(MM,I),MM=1,NM)
116 FORMAT (1X,I4,2X,20F6.4)
36 CONTINUE
IF(NRUNS.GT.0) GO TO 1
GO TO 999
38 PRINT 444
444 FORMAT (//,* OPTION NOT INSTALLED*)
90 PRINT 998
998 FORMAT (//,* ITERATIONS FOR F EXCEEDED 50 *)
999 STOP & END

FUNCTION EVAL(F)
COMMON M S REAL M
EVAL=(1.0-EXP(-F-M)) * F/(F+M)
RETURN S END

SUBROUTINE OUTISO(JT)
COMMON M,IBT,IET,EINC,NE,FST(20),FT(20),IS(50,50),IY(50,50)
1,KARD
REAL M
DIMENSION JT(50,50)
NN=-1
DO 200 N=IBT,IET
NN=NN+1
I=IET-NN
200 PRINT 201,I,(JT(I,J),J=1,NE)
201 FORMAT (//,2X,I2,2X,20I6)
TEM=-EINC
DO 202 N=1,NE
TEM = TEM+EINC

```

```

202 FT(N) = TEM
   PRINT 203, (FT(N), N=1, NE)
203 FORMAT (///, * E      *, 20F6.3)
   PRINT 204, (FST(N), N=1, NE)

204 FORMAT (* F      *, 20F6.3)
   PRINT 205
205 FORMAT (/, 5X, * E = EXPLOITATION RATE, F = INST. FISHING MORT. RATE*)
   IF (KARC.EG.0) GO TO 210
   DO 206 I=1BT, IET
206 PUNCH 207, (JT(I, J), J=1, NE)
207 FORMAT (10I8, /, 10I8)
   PUNCH 208
208 FORMAT (/)
210 RETURN 3 END

```

TYPICAL INPUT FOR ISOE

```

2          NUMBER OF RUNS
BOCACCIO ROCKFISH      DATA FROM PHILLIPS(1964) CFG FISH BULL. 126
APRIL 14, 1976      RH PARRISH
  1 30  1 10 .200 .050  3 .020 20
    812.97      .14784      -0.6439 .0000000012860      3.0941
000000000000      .1      .5      .8  1.0  1.0  1.0  1.0  1.0
CHILEPEPPER ROCKFISH      DATA FROM PHILLIPS(1964) CFG FISH BULL. 126
APRIL 14, 1976      RH PARRISH
  1 16  1 10 .300 .050  3 .020 20
    552.67      .18204      -0.2283 .0000000006260      3.2438
000000      .05      .3      .5      .8  1.0  1.0  1.0  1.0  1.0

```

APPENDIX II. QUOTA SIMULATION PROGRAM.

PROGRAM QUOTAE--(INPUT,OUTPUT,PUNCH)

C QUOTA SIMULATION MODEL RH PARRISH JUNE 15,1976

C CONTROL CARD VARIABLE DESCRIPTIONS

C ITO BEGINNING YEAR OF THE SIMULATION
 C NYRS NUMBER OF YEARS FOR THE SIMULATION
 C IBT MINIMUM AGE AT RECRUITMENT
 C IET MAXIMUM AGE AT RECRUITMENT
 C MAXA MAXIMUM AGE
 C IRUN CONTROL FOR OUTPUT
 C IRUN=0 OUTPUT IS LIMITED TO YIELD MATRICES
 C IRUN=1 OUTPUT IS ANNUAL SPAWNING BIOMASS + YIELD MATRICES
 C IRUN=2 OUTPUT IS ANNUAL SPAWNING BIOMASS, YIELD, TOTAL
 C BIOMASS AND RECRUIT BIOMASS + YIELD MATRICES
 C ILOGI ILOGI=0 FOR CONSTANT PS(1)
 C ILOGI=1 FOR DENSITY DEPENDENT PS(1)
 C IENV IENV= THE NUMBER OF ENVIRONMENTAL VARIABLES INPUT
 C MAXIMUM NUMBER IS 6, FORMAT STATEMENT 152
 C IENV=0 IF NO ENVIRONMENTAL VARIABLES ARE INPUT
 C IPRO IPRO=0, =1, =2 DEPENDING ON THE NO. OF PRORATED
 C ENVIRONMENTAL VARIABLES, FORMAT STATEMENTS 163,164
 C IQSET SETS THE BIOMASS SEGMENT THAT THE QUOTA IS BASED ON
 C IQSET=0 QUOTA BASED ON SPAWNING BIOMASS
 C IQSET=1 QUOTA BASED ON TOTAL BIOMASS
 C IQSET=2 QUOTA BASED ON AGE I + AGE II BIOMASS
 C RMAX MAXIMUM RECRUIT BIOMASS ALLOWED
 C QAL LOWER QUOTA LEVEL
 C QBL UPPER QUOTA LEVEL
 C M INSTANTANEOUS NATURAL MORTALITY RATE
 C SLP SUBLEGAL PROPORTION (SETS CATCH OF UNDERSIZED FISH)
 C QA LOWER QUOTA PROPORTION
 C QMIN MINIMUM UPPER QUOTA PROPORTION
 C QINC INCREMENT FOR UPPER QUOTA PROPORTION
 C NQ NUMBER OF QUOTA PROPORTIONS
 C BPOP(N) BEGINNING BIOMASS BY AGE GROUP
 C PS(N) PROPORTION SPAWNING BY AGE GROUP
 C G(N) PROPORTION ANNUAL GROWTH BY AGE GROUP
 C GH(N) PROPORTION GROWTH FOR HALF OF THE YEAR BY AGE GROUP
 C (IE AVERAGE GROWTH TO CAPTURE)

COMMON

OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
 1Q2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
 2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
 3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
 4TREC(100),TSPOP(100),TYIELD(100),ITPOP(100),G(51),GH(51),
 5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
 REAL H
 INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,ITPOP
 READ 001,KL
 001 FORMAT(I2)
 DO 199 KLM=1,KL
 READ 100,I0,NYRS,IBT,IET,MAXA,IRUN,ILOGI,IENV,IPRO,IQSET,
 1RMAX,QAL,QBL,M,SLP,QA,QMIN,QINC,NQ
 100 FORMAT (10I4,/,3F8.0,5F4.2,14)
 IF(KLM.GT.1) GO TO 102
 READ 101,(BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
 101 FORMAT (F6.3,3F6.4)
 102 PRINT 103,M,NYRS,I0

```

103 FORMAT      (*1TWO STEP QUOTA SIMULATION MODEL FOR *,
1*PACIFIC HACKEREL  RH PARRISH  MAY 18, 1976*
1,/,* ALL POP FIGURES IN THOUSANDS OF POUNDS*
3,/,* NATURAL MORTALITY  M=*,F4.2,/,* SIMULATED FOR  *,I4,* YEARS*
4,/,* STARTING POPULATION *,I4,/,* MODEL PARAMETERS BY AGE GROUP*
5,/,* AGE      STARTING  PROPORTION  PROPORTION  PROPORTION
6GROWTH*,/,* GROUP  POPULATION  SPAWNING  ANNUAL GROWTH  T
70 CAPTURE*)
  PRINT 104,(N,BPOP(N),PS(N),G(N),GH(N),N=IBT,MAXA)
104 FORMAT(I2,F13.3,F12.3,F15.3,F18.3)
105 FORMAT(//,60H EXTINCTION CURVE FOR PS(1)=0.54*EXP(-.0003071709*TPO
1P) )
  IF (ILOGI.EQ.1) PRINT 105
  IF (IQSET=1) 106,108,110
106 PRINT 107
107 FORMAT(//,* QUOTA BASED ON SPAWNING BIOMASS*)
  GO TO 112
108 PRINT 109
109 FORMAT(//,* QUOTA BASED ON TOTAL BIOMASS*)
  GO TO 112
110 PRINT 111
111 FORMAT(//,* QUOTA BASED ON THE BIOMASS OF AGEI + AGEII*)
112 PRINT 113,QAL,QA,QBL
113 FORMAT (//,* LOWER QUOTA LEVEL =*,F8.0,/,* LOWER QUOTA PROPORTION=
1*,F6.3,/,* UPPER QUOTA LEVEL = *,F8.0)
  PRINT 114
114 FORMAT (//,* RECRUITMENT MODEL*,//,1X,
1* RICKER BMDPSR TRANSPORT MODEL*,/,
  PRINT 115,IBT,IET,IRUN,ILOGI,IENV,IPRO,IQSET,RMAX,SLP,MAXA,QMIN,
  IQINC,NQ
115 FORMAT(//,* IBT=*,I4,/,* IET=*,I4,/,* IRUN=*,I4,/,* ILOGI=*,I4,/,
1*,IENV=*,I4,/,* IPRO=*,I4,/,* IQSET=*,I4,/,* RMAX=*,F8.0,/,
2* SLP=*,F4.2,/,* MAXA=*,I4,/,* QMIN=*,F5.3,/,* QINC=*,F5.3,/,
3* NQ=*,I4)
  IF (KLM.GT.1) GO TO 119
  IF (IENV.GT.0) GO TO 150
  IF (IPRO.GT.0) GO TO 150
116 CONTINUE

C  BODY STARTS HERE
119 IF (NQ.EQ.1) GO TO 120
  GO TO 122
120 IU=-9
  DO 121 N=IBT,IET
121 CALL MACQE
  CALL OUTM
  STOP
122 IU=NQ $ QB=QMIN-QINC $ NL=IET-IBT+1
  DO 124 IQB=1,NQ
  QB=QB+QINC $ L=0
  DO 123 J=IBT,IET
  L=L+1
  CALL MACQE
  MAT(L,IQB)=TYIELD(L)/NYRS
123 MA(L,IQB)=ACATCH
124 CALL OUTM
  PRINT 125,NYRS
125 FORMAT (1H1,/,20X,I4,* YEAR MEAN YIELD*)
  CALL OUTMAT(MAT)
  IT=I10+NYRS-1
  PRINT 126,IT
126 FORMAT (1H1,/,20X,*YIELD IN *,I4)
  CALL OUTMAT(MA)
  GO TO 199
150 IF (IENV.LT.1) GO TO 160
  DO 151 N=1,NYRS

```



```

151 READ 152, (ENV(N, NN), NN=1, IENV)
152 FORMAT(6F8.2)
160 IF (IPRO.GT.0) GO TO 161
    GO TO 116
161 DO 162 N=1, NYRS
162 READ 163, (ENV(N, NN), NN=7, 9)
163 FORMAT(35X, 3F5.0)
    IF (IPRO.EQ.1) GO TO 116
    DO 164 N=1, NYRS
164 READ 165, (ENV(N, NN), NN=10, 12)
165 FORMAT(35X, 3F5.0)
    GO TO 116
199 CONTINUE
    STOP & END

```

SUBROUTINE MACQE COMMON

```

OITO, NYRS, TPOP, PS(51), POPA(51), P(12), ENV(100, 12), IMEAN(100, 12),
1Q2, QA, QB, QAL, QBL, QPOP, SUBQ, CQ, SLP, MAXA, SUBPOP, I, J, POPC(51), SPOP,
2REC, IBT, IET, IU, IRUN, ILOGI, IENV, IPRO, M, IQSET, RMAX, QMIN, QINC, NQ,
3MAT(16, 16), MA(16, 16), B0, B1, B2, B4, ACATCH, XMORT(51), NENV, L, NL,
4TREC(100), TSPOP(100), TYIELD(100), TTPOP(100), S(51), GH(51),
5AREC(100, 16), ASPOP(100, 16), AYIELD(100, 16), ATPOP(100, 16), BPOP(51)
REAL M
INTEGER ASPOP, AYIELD, AREC, ATPOP, TSPOP, TYIELD, TREC, TTPOP
TSPOP(L) = TREC(L) = TYIELD(L) = TTPOP(L) = 0
DO 500 N=IBT, MAXA
500 POPA(N) = BPOP(N)
    DO 516 I=1, NYRS
    SPOP = ACATCH = TPOP = 0
    DO 501 N=IBT, MAXA
    POPC(N) = POPA(N) * GH(N)
501 TPOP = TPOP + POPA(N)
    IF (ILOGI.EQ.1) CALL LOGI
    DO 502 N=IBT, MAXA
502 SPOP = SPOP + POPA(N) * PS(N)
    CALL FUN
    IF (IQSET-1) 503, 504, 505
503 Q2 = SPOP & GO TO 505
504 Q2 = TPOP & GO TO 506
505 Q2 = POPA(1) + POPA(2)
506 IF (Q2.LT.QAL) GO TO 507
    GO TO 508
507 Z = M & A = 1.0 - EXP(-Z)
    DO 58 N=IBT, MAXA
58 XMORT(N) = POPA(N) * A
    GO TO 512
508 CALL QUOT
    E = CQ/QPOP
    F = FVAL(E, M)
    Z = F + M & A = 1.0 - EXP(-Z)
    DO 509 N=J, MAXA
    XMORT(N) = POPA(N) * A
509 ACATCH = ACATCH + XMORT(N) * (F/Z) * GH(N)
    IF (J.GT.IBT) GO TO 513
    GO TO 512
510 E = SUBQ/SUBPOP
    F = FVAL(E, M)
    ZS = F + M & AS = 1.0 - EXP(-ZS)
    JT = J - 1
    DO 511 N=IBT, JT
    XMORT(N) = POPA(N) * AS
511 ACATCH = ACATCH + XMORT(N) * (F/ZS) * GH(N)
512 NT = MAXA + 2
    DO 513 N=IBT, MAXA

```

```

      NT=NT-1
513 POPA(NT)=(POPA(NT-1)-XMORT(NT-1)) * G(NT-1)
      POPA(MAXA) = POPA(MAXA) + POPA(MAXA+1)
      POPA(1BT)=REC
      TSPOP(L)=TSPOP(L) + SPOP
      TREC(L) = TREC(L) + REC
      TYIELD(L) = TYIELD(L) + ACATCH
      TTPOP(L) = TTPOP(L) + TPOP
      ASPOP(I,L) = SPOP
      AREC(I,L) = REC
      AYIELD(I,L) = ACATCH
      ATPOP(I,L) = TPOP
      IF(REC.GT.RMAX) GO TO 514
      GO TO 516
514 PRINT 515
515 FORMAT (* RECRUITMENT BLEWUP OR FAILED*)
      CALL OUTM
      STOP
516 CONTINUE
517 RETURN $ END

```

```

      SUBROUTINE FUN
      COMMON

```

```

      OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
      1Q2,QA,QB,QAL,QBL,OPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,1BT,IET,IU,IRUN,ILOGI,IENV,IPRO,M,IQSET,RMAX,QMIN,QINC,NQ,
      3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M

```

```

      IF(IPRO.EQ.0) GO TO 666
      P(1)=(PS(1)*POPA(1))/SPOP
      P(2)=(PS(2)*POPA(2))/SPOP
      P(3)=(PS(3)*POPA(3) +POPA(4) +POPA(5) +POPA(6))/SPOP
      PROA=P(3)*ENV(I,7)+P(2)*ENV(I,8) + P(1)*ENV(I,9)
      IF(IPRO.EQ.2) PROB=P(3)*ENV(I,10)+P(2)*ENV(I,11)+P(1)*ENV(I,12)

```

```

666 CONTINUE

```

```

C RECRUITMENT MODEL AFTER THIS CARD
2* REC= 0.97815*SPOP*EXP(-0.000037741*SPOP)*EXP(0.020787*PROA)
3 *EXP(0.0039065*PROB) *)
      RETURN $ END

```

```

      SUBROUTINE HOOPS

```

```

C THIS SUBROUTINE MODELS THE MAIN THESES PROBLEM
      GRADOFF = HASSLE ** EXP( NSEC + NADMIN )

```

```

300 DO 388 N=1,PHD

```

```

310 PLACE = GRADOFF

```

```

      DO 311 I=1,LUNCH

```

```

      IF(SEC.LT.HAPPY.OR.ADMIN.LT.DUNCE) WAIT = HOUR

```

```

311 CONTINUE

```

```

      GO TO 330

```

```

320 MAIL=GRADOFF

```

```

330 IF(MARGINS.GT.ALLOWED) TYPE = 106

```

```

      CENTERED = CENTERED +(INCH / 4)

```

```

      IF (TITLE.LT.CENTERED) GO TO 332

```

```

331 DELAY = 365 * SHAFT ** 2

```

```

      GO TO 333

```

```

332 TYPE = 1.0

```

```

      COPIES = 6

```

```

      GO TO 300

```

```

333 IF(OUTPUT.GT.MARGINS) GO TO 334

```

```

      GO TO 335

```

```

      PROBLEM = GRADOFF

```

```

334 APPENDIX = XEROX * 3.75 * 13

```

```

      COPIES = 6

```

```

      GO TO 320

```

```

335 TIME = (DAYS**3) * EXP(1.0 + COFFEE)

```

```

      DOLLARS = TIME

```

```

      IF (XEROX.LT.DARK) GO TO 334
      MAIL = DELAY = DOLLARS
388  CONTINUE
      TYPIST = QUIT
      IF (TERM.NE.OVER) GO TO 399
      DOLLARS = TUITION + (FOOD * 4) + RENT(I,N) + (MISC * 4)
      GO TO 300
399  STOP

```

```

C      FUNCTION FVAL(E,M)
C      ITERATIVE SOLUTION FOR INST. FISHING MORE-GIVEN EXPLOITATION RATE
C      AND INST. NATURAL MORT.
      COMMON ITO, NYRS
      REAL M
      F=E $ N=0
      IF (E.EQ.0) GO TO 2
1     N=N+1 $ IF (N.GT.5) GO TO 90
      F1=F-0.01 $ F2=F+0.01
      EV=(1.0 - EXP(-F-M)) * F / (F+M)
      E1=(1.0 - EXP(-F1-M)) * F1 / (F1+M)
      E2=(1.0 - EXP(-F2-M)) * F2 / (F2+M)
      SLOPE= (E2-E1) / 0.02
      DIFFE = EV-E
      F=F - DIFFE / SLOPE
      IF (ABS(DIFFE).GT.0.000001) GO TO 1
2     FVAL=F
      RETURN
90  PRINT 900
900  FORMAT(//,* ITERATIONS FOR F EXCEEDED 50*)
991  STOP $ END

```

```

C      SUBROUTINE LOGI
      PACIFIC MACKEREL SUBROUTINE
      COMMON
      ITO, NYRS, TPOP, PS(51), POPA(51), P(12), ENV(100,12), IMEAN(100,12)
      PS(1)=.54*EXP(-.0000071709*TPOP)
      RETURN $ END

      SUBROUTINE QUOT
      COMMON
      ITO, NYRS, TPOP, PS(51), POPA(51), P(12), ENV(100,12), IMEAN(100,12),
      IQ2,QA,QB,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
      2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPOD,M,IQSET,RMAX,QMIN,QINC,NQ,
      3MAT(15,15),MA(15,15),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL
      REAL M
      IF (Q2.GT.QBL) GO TO 900
      QUO=QA*(Q2-QAL)
      GO TO 901
900  QUO=(QBL-QAL)*QA + (Q2-QBL)*QB
901  QPOP=SUBQ*0.01 $ SUBPOP=0.1
      DO 902 IC=J,MAXA
902  QPOP=QPOP+POPC(IC)
      IF (J.EQ.IBT) GO TO 904
      JJ=J-1
      DO 903 IC=1,JJ
903  SUBPOP=SUBPOP + POPC(IC)
      SUBQ=SLP*QUO
      QUO=QUO-SUBQ
      IF (QUO/QPOP.GT.1.0) GO TO 905
904  CQ=QUO $ GO TO 906
905  CQ=QPOP
906  IF (SUBQ/SUBPOP.LT.0.5) GO TO 907
      X=0.5*SUBPOP $ Y=SUBQ-X
      SUBQ=X $ CQ=QUO+Y
907  RETURN $ END

```

```

SUBROUTINE OUTM
COMMON
OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
1Q2,QA,Q3,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPOD,M,IQSET,RMAX,QMIN,QINC,NQ,
3MAT(16,16),MA(15,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
REAL M
INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
IF(REC.ST.RMAX) GO TO 606
IF(IRUN.EQ.0) GO TO 609
IOK=1
IF(QBL.LT.1.AND.IQSET.EQ.1) IOK=0
IF(IOK.EQ.1) PRINT 600,QB
IF(IOK.NE.1) PRINT 601,QB
600 FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, UPPER QUOTA PROPORTION =*,
1,F6.3)
601 FORMAT(//,T21,*ANNUAL SPAWNING BIOMASS, EXPLOITATION RATE =*,F6.3)
CALL OUTP (ASPOP,TSPOP)
IF(IRUN.EQ.1) GO TO 609
IF(IOK.EQ.1) PRINT 602,QB
IF(IOK.NE.1) PRINT 603,QB
602 FORMAT (//,T21,*ANNUAL YIELD, UPPER QUOTA PROPORTION =*,F6.3)
603 FORMAT (//,T21,*ANNUAL YIELD, EXPLOITATION RATE =*,F6.3)
CALL OUTP (AYIELD,TYIELD)
IF(IOK.EQ.1) PRINT 604,QB
IF(IOK.NE.1) PRINT 605,QB
604 FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, UPPER QUOTA PROPORTION =*,
1,F6.3)
605 FORMAT (//,T21,*ANNUAL TOTAL BIOMASS, EXPLOITATION RATE =*,F6.3)
CALL OUTP (ATPOP,TTPOP)
606 CONTINUE
IF(IOK.EQ.1) PRINT 607,QB
IF(IOK.NE.1) PRINT 608,QB
607 FORMAT (//,T21,*ANNUAL RECRUITMENT, UPPER QUOTA PROPORTION =*,
1,F6.3)
608 FORMAT (//,T21,*ANNUAL RECRUITMENT, EXPLOITATION RATE =*,F6.3)
CALL OUTP (AREC,TREC)
609 RETURN $ END

```

```

SUBROUTINE OUTP (IANN,ITOT)
COMMON
OITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
1Q2,QA,Q3,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
2REC,IBT,IET,IU,IRUN,ILOGI,IENV,IPOD,M,IQSET,RMAX,QMIN,QINC,NQ,
3MAT(16,16),MA(15,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
REAL M
INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
DIMENSION IANN(100,16),ITOT(100)
PRINT 700,(N,N=IBT,IET)
700 FORMAT(////,T21,*AGE AT RECRUITMENT*,//,* SEASON*,16I8)
IS=ITO-1
DO 701 N=1,NYRS
IS=IS+1
701 PRINT 702,IS,(IANN(N,K),K=1,NL)
702 FORMAT (1X,I4,2X,16I8)
IF(IU.NE.-9) RETURN
DO 703 N=IBT,IET
703 ITOT(N) = ITOT(N)/NYRS
PRINT 704,(ITOT(N),N=IBT,IET)
704 FORMAT (* MEAN *,16I8)
RETURN $ END

```

```

SUBROUTINE OUTMAT(MT)
COMMON
DITO,NYRS, TPOP,PS(51),POPA(51),P(12),ENV(100,12),IMEAN(100,12),
1Q2,QA,Q3,QAL,QBL,QPOP,SUBQ,CQ,SLP,MAXA,SUBPOP,I,J,POPC(51),SPOP,
2REC,IET,IET,IU,IRUN,ILOGI,IENV,IPO,M,IQSET,RMAX,QMIN,QINC,NO,
3MAT(16,16),MA(16,16),B0,B1,B2,B4,ACATCH,XMORT(51),NENV,L,NL,
4TREC(100),TSPOP(100),TYIELD(100),TTPOP(100),G(51),GH(51),
5AREC(100,16),ASPOP(100,16),AYIELD(100,16),ATPOP(100,16),BPOP(51)
REAL M
INTEGER ASPOP,AYIELD,AREC,ATPOP,TSPOP,TYIELD,TREC,TTPOP
DIMENSION MT(16,16),QQ(16)
PRINT 800
800 FORMAT (* AGE*,/,* AT*,/,* REC.*)
K=IET+1
DO 801 NJ=1,NL
K=K-1
C PUNCH CARD OUTPUT FOR YIELD ISOPLETH PLOTS
PUNCH 008,(MT(K,N),N=1,NQ)
808 FORMAT (10I8)
801 PRINT 802 ,K,(MT(K,N),N=1,NQ)
802 FORMAT (///,1X,I2,4X,16I8)
PRINT 803
803 FORMAT (///,7X)
QY=QMIN-QINC
DO 804 N=1,NQ
QY=QY+QINC
804 QQ(N)=QY
PRINT 805,(QQ(N),N=1,NQ)
805 FORMAT (7X,16F8.2)
IF(IQSET.NE.1) GO TO 807
IF(QBL.LT.1.0) PRINT 806
806 FORMAT(/,T32,*EXPLOITATION RATE*)
IF(QBL.LT.1.0) GO TO 899
807 PRINT 808
808 FORMAT(/,T32,*QUOTA PROPORTION*)
899 RETURN $ END

```

TYPICAL INPUT FOR QUOTAE

		NUMBER OF RUNS											
4	30	1	5	6	2	1	0	2	0				
1946	30	1	5	6	2	1	0	2	0				
900000.	20000.	40000.	.50	.10	.20	.00	.05	10					
18933	.60	1.649	1.316										
51286	.77	1.508	1.207										
30137	.88	1.282	1.143										
143911	.90	1.2	1.103										
167831	.00	1.146	1.076										
01.00	1.109	1.057											
30N 119W 1946		110	80	132	155	252	347	207	201	207	86	54	53
30N 119W 1947		110	60	111	191	114	176	243	152	102	95	70	61
30N 119W 1948		30	102	82	61	220	151	126	119	105	81	72	31
30N 119W 1949		63	121	90	150	158	163	113	155	123	91	84	53
30N 119W 1950		60	58	117	151	153	164	76	121	101	70	58	88
30N 119W 1951		112	85	115	91	204	207	157	120	155	128	73	49
30N 119W 1952		24	35	108	99	224	150	84	115	98	107	54	31
30N 119W 1953		56	125	158	183	218	235	143	191	154	139	128	113
30N 119W 1954		77	94	77	174	173	210	108	178	164	105	69	49
30N 119W 1955		81	68	99	226	265	299	202	173	242	173	111	61
30N 119W 1956		72	98	207	165	238	297	191	245	180	139	60	52
30N 119W 1957		20	56	165	184	193	274	202	170	167	122	93	71
30N 119W 1958		105	75	101	229	191	258	185	130	165	130	115	57

30N 119W 1959	99	33	168	149	231	304	195	139	151	153	64	27
30N 119W 1960	45	100	159	144	299	133	111	138	133	121	47	66
30N 119W 1961	33	157	163	164	210	159	94	124	70	66	47	53
30N 119W 1962	49	46	82	189	212	218	155	166	148	97	103	32
30N 119W 1963	9	63	87	115	150	163	182	131	93	71	63	41
30N 119W 1964	69	63	149	169	225	204	175	134	118	60	38	73
30N 119W 1965	44	54	50	39	185	142	95	74	59	58	1	27
30N 119W 1966	44	49	72	64	81	121	132	61	76	51	14	42
30N 119W 1967	29	65	56	73	163	130	123	156	71	91	13	58
30N 119W 1968	32	30	92	116	152	157	162	168	104	76	90	32
30N 119W 1969	8	45	135	185	227	194	219	202	173	134	7	70
30N 119W 1970	27	13	96	183	241	238	177	225	158	117	55	45
30N 119W 1971	82	164	166	232	241	265	196	147	170	142	139	82
30N 119W 1972	91	88	186	180	165	168	125	113	90	61	87	85
30N 119W 1973	64	7	178	192	155	173	137	149	121	90	93	97
30N 119W 1974	22	104	93	234	284	263	147	167	141	104	74	34
30N 119W 1975	50	62	127	174	187	197	192	194	180	146	134	58
30N 119W 1946 ODI	467	30	68	-201	-658	-578	-254	-69	-51	-51	83	34
30N 119W 1947 ODI	-78	48	-114	-140	-362	-303	-107	-274	-124	-46	232	104
30N 119W 1948 ODI	-75	68	-55	-270	-322	-338	-117	-100	-75	93	215	26
30N 119W 1949 ODI	102	125	-188	-167	-309	-105	-137	-56	50	78	184	87
30N 119W 1950 ODI	-75	-78	54	-206	-346	-356	-52	-120	-247	-141	3	-26
30N 119W 1951 ODI	-113	-36	84	-211	-449	-374	-162	-169	-256	12	-4	66
30N 119W 1952 ODI	-20	-68	-42	-55	-330	-278	-342	-134	-221	-152	-57	-17
30N 119W 1953 ODI	63	246	-255	-441	-439	-595	-362	-594	-532	-284	-121	166
30N 119W 1954 ODI	-31	-66	-166	-492	-455	-459	-195	-528	-118	-229	47	-75
30N 119W 1955 ODI	21	-35	-116	-370	-570	-657	-276	-119	-199	-230	108	-81
30N 119W 1956 ODI	23	-62	-26	-324	-532	-424	-402	-371	-137	-146	170	110
30N 119W 1957 ODI	-26	-181	-205	-393	-468	-363	-273	-205	-448	-213	-51	-19
30N 119W 1958 ODI	-123	-294	-397	-311	-834	-865	-608	-364	-183	-51	19	57
30N 119W 1959 ODI	-5	-89	-100	-405	-656	-671	-418	-407	-279	-38	57	61
30N 119W 1960 ODI	-54	-141	-245	-120	-409	-380	-233	-196	-57	-1	-4	76
30N 119W 1961 ODI	54	-59	-248	-112	-742	-652	-285	33	-40	58	-4	165
30N 119W 1962 ODI	173	-96	-125	-183	-592	-284	-785	-563	-308	-283	-88	13
30N 119W 1963 ODI	-20	-121	-336	-524	-613	-814	-875	-524	94	5	46	79
30N 119W 1964 ODI	102	36	-246	-818	-1960	-2005</						

APPENDIX III. UPDATE FOR CDC VERSION OF BMOP3R NONLINEAR REGRESSION.

```

*ID MAY25
*D P3RJUL.2
*I BMOP3R.25
  X MAY 25, 1976 PEG
*D BMOP3R.34
*I BMOP3R.33
  CTOL=1.0E-8
*D UNCOLA.73
*I UNCOLA.72
  X 50H TOLERANCE FOR CONVERGENCE
*D P3RJUL.24
*I P3RJUL.23
  1 F20.5)
*D RITEIT.15
*I RITEIT.14
  3000 FORMAT(2X,I4,7X,I4,F21.6,1X,F18.7,5(1X,F14.9))
*D REDEV.18
*I REDEV.17
  3000 FORMAT(1X,I4,2X,A1,A8,1X,F14.6,1X,F14.6,2(2X,F13.6))
*D RITEND.28
*I RITEND.27
  900 FORMAT(2X,I4,7X,I4,F21.6,4X,6(1X,F14.6))
*D RITEND.48,RITEND.53
*I RITEND.47
  5600 FORMAT(1H0,2X,7H CASE ,10HPREDICTED ,7X,
    * 10HSTD DEV OF,5X,8HOBERVED/
    * 10X,A8,9X,10HPRED VALUE,
    * 5X,A8,9X,A8,4(7X,A8))
  5800 FORMAT(1X,I4,A2,F13.6,2X,F15.5,2X,F13.6,
    * 2X,F15.6,4(2X,F13.6))
*I RITEND.96
  IF(ISFUN.GT.5) GO TO 47
*D FUN.10
*I FUN.9
  IF(ISFUN.GE.1.AND.ISFUN.LE.19)GO TO (100,200,300,400,500,600,700,
    *800,900,1000,1100,1200,1300,1400,1500,1600,1700,1800,1900),ISFUN
*I FUN.99
C
C RICKER MODEL
600 F=P(1)*X(1)*EXP(P(2)*X(1))
  DF(1)=X(1)*EXP(P(2)*X(1))
  DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))
  RETURN
C
C CUSHING MODEL
700 F=P(1)*X(1)**P(2)
  DF(1)=X(1)**P(2)
  DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))
  RETURN
C
C CLARK-RICKER MODEL
800 F=P(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
  DF(1)=X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
  DF(2)=P(1)*X(1)*X(1)*EXP(P(2)*X(1))*EXP(P(3)/X(1))
  DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) * (1/X(1)) * EXP(P(3)/X(1))
  RETURN

```

```

C
C CLARK-CUSHING MODEL
900 F=P(1)*X(1)**P(2)*EXP(P(3)/X(1))
   DF(1)=X(1)**P(2)*EXP(P(3)/X(1))
   DF(2)=P(1)*X(1)**P(2)*ALOG(X(1))*EXP(P(3)/X(1))
   DF(3)=P(1)*X(1)**P(2) *(1/X(1)) * EXP(P(3)/X(1))
   RETURN
C
C CUSHING TRANSPORT MODEL
1000 F=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
   DF(1)=X(1)**P(2)*EXP(P(3)*X(2))*EXP(P(4)*X(3))
   DF(2)=P(1)*X(1)**P(2)*ALOG(X(1)) *EXP(P(3)*X(2)) *EXP(P(4)*X(3))
   DF(3)=P(1)*X(1)**P(2) *X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
   DF(4)=P(1)*X(1)**P(2)*EXP(P(3)*X(2))*X(3)*EXP(P(4)*X(3))
   RETURN
C
C CUSHING SEA LEVEL MODEL
1100 F=P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
   1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
   DF(1) = X(1)**P(2) * EXP( P(3)*X(2) )
   1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
   DF(2) = P(1)*X(1)**P(2)*ALOG(X(1)) * EXP( P(3)*X(2) )
   1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
   DF(3) = P(1)*X(1)**P(2) * X(2)*EXP( P(3)*X(2) )
   1 *EXP(P(4)*X(3) ) * EXP( P(5)*X(4) )
   DF(4) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
   1 *X(3)*EXP( P(4)*X(3) ) * EXP( P(5)*X(4) )
   DF(5) = P(1)*X(1)**P(2) * EXP( P(3)*X(2) )
   1 *EXP( P(4)*X(3) ) * X(4)*EXP( P(5)*X(4) )
   RETURN
C
C EXPONENTIAL MODEL
C
1200 F = P(1) * EXP( P(2)*X(1) )
   DF(1) = EXP( P(2)*X(1) )
   DF(2) = P(1) * X(1) * EXP(P(2)*X(1))
   RETURN
C
C RECRUIT PER SPANNER TRANSPORT MODEL
C
1300 F = P(1) * EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(1) = EXP(P(2)*X(1)) * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(2) = P(1)*X(1)*EXP(P(2)*X(1)) *EXP(P(3)*X(2)) *EXP(P(4)*X(3))
   DF(3) = P(1)*EXP(P(2)*X(1)) *X(2)*EXP(P(3)*X(2)) *EXP(P(4)*X(3))
   DF(4) = P(1)*EXP(P(2)*X(1)) *EXP(P(3)*X(2)) * X(3)*EXP(P(4)*X(3))
   RETURN
C
C RICKER TRANSPORT MODEL
C
1400 F = P(1)*X(1)*EXP(P(2)*X(1))
   1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(1) = X(1) * EXP(P(2)*X(1))
   1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(2) = P(1) * X(1) * X(1) * EXP(P(2)*X(1))
   1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(3) = P(1) * X(1) * EXP(P(2)*X(1)) * X(2)
   1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3)
   1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3))
   RETURN
C
C RICKER SEA LEVEL MODEL

```


C

```

1500 F = P(1) * X(1) * EXP(P(2)*X(1))
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(1) = X(1) * EXP(P(2)*X(1))
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(2) = P(1) * X(1) * EXP(P(2)*X(1)) * X(1)
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(3) = P(1) * X(1) * EXP(P(2)*X(1)) * X(2)
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(4) = P(1) * X(1) * EXP(P(2)*X(1)) * X(3)
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      DF(5) = P(1) * X(1) * EXP(P(2)*X(1)) * X(4)
      1 * EXP(P(3)*X(2)) * EXP(P(4)*X(3)) * EXP(P(5)*X(4))
      RETURN

```

C

C

CLARK-RICKER TRANSPORT MODEL

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1600 F=P(1)*X(1) *EXP(P(2)*X(1)) * EXP(P(3)/X(1))
      1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(1)= X(1) *EXP(P(2)*X(1)) * EXP(P(3)/X(1))
      1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(2)= P(1)*X(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
      1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(3)=P(1)*X(1)*EXP(P(2)*X(1)) * (1.0/X(1)) * EXP(P(3)/X(1))
      1* EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(4)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
      1*X(2) * EXP(P(4)*X(2)) * EXP(P(5)*X(3))
      DF(5)=P(1)*X(1) * EXP(P(2)*X(1)) * EXP(P(3)/X(1))
      1* EXP(P(4)*X(2)) * X(3) * EXP(P(5)*X(3))
      RETURN

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1700 RETURN

1800 RETURN

1900 RETURN